SPECIES LIMITS AND PHYLOGENETIC RELATIONSHIPS IN THE DIDELPHID MARSUPIAL GENUS *THYLAMYS* BASED ON MITOCHONDRIAL DNA SEQUENCES AND MORPHOLOGY

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ABSTRACT

Species of the didelphid marsupial genus *Thylamys*, commonly known as fat-tailed mouse opossums, are broadly distributed in the open habitats of central and southern South America. In this report we examine species limits in the genus and infer phylogenetic relationships among *Thylamys* species using both molecular phylogenetic and morphological methods. We assessed species limits using a broad geographic sample of DNA sequences from the mitochondrial gene cytochrome *b* in conjunction with morphological character analysis, and we inferred phylogenetic relationships among species using the cytochrome-*b* dataset in addition to sequences from the mitochondrial genes cytochrome *c* oxidase subunit II and NADH dehydrogenase 2 for a representative subset of individuals. Based on the results of these analyses, we recognize *Xerodelphys* (new subgenus) for *T. karimii* and *T. velutinus*, and we recognize seven valid species in the nominotypical subgenus. The latter includes *T. macrurus, T. pusillus*, and two monophyletic species groups: the Elegans Group (*T. elegans, T. pallidior, T. tatei*) and the Venustus Group (*T. sponsorius, T. venustus*). Analysis of cytochrome-*b* sequences additionally reveals deep phylogeographic structuring in three species (*T. pallidior*, *T. pusillus*, *T. venustus*), each of which contains two or three robustly supported allopatric haplogroups. The existence of undescribed Peruvian forms of the Elegans Group is also plausibly indicated. We provide morphological diagnoses of all species recognized as valid in this report, summarize information about geographic distributions, comment on previous misidentifications, and briefly consider historical-biogeographic scenarios with a focus on dispersal events across the Andes.

INTRODUCTION

Species of the didelphid marsupial genus *Thylamys*, commonly known as fat-tailed mouse opossums, are widely distributed in savanna woodlands, thornscrub, semidesert shrublands, shrubby steppe, montane thickets, and other more or less open, nonforest habitats from western Peru and eastern Brazil southward to central Chile and Patagonia. Their common English name refers to the seasonal deposition of caudal fat (fig. 1), a phylogenetically derived trait that *Thylamys* shares with its sister taxon *Lestodelphys* (see Morton, 1980). Together, *Thylamys*, *Lestodelphys*, and four other didelphid genera (*Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Marmosops*) comprise the tribe Thylamyini, one of two well-supported suprageneric groups of small, mouselike or "murine" opossums (Voss and Jansa, 2009).

Although the family Didelphidae is a predominantly lowland rainforest clade, *Thylamys* is the most species-rich and widely distributed of several opossum lineages that invaded nonforest habitats in the Miocene (Jansa et al., in prep.). Because geographic patterns of endemism and cladogenesis among fat-tailed mouse opossums are potentially informative about the late Tertiary history of nonforest environments in South America, the systematics of this group are of considerable biogeographic interest. Unfortunately, neither the number of valid species in the genus nor their evolutionary relationships has been convincingly resolved by previous studies.

Taxonomic History

Most of the nominal taxa now included in *Thylamys* were referred to the "Elegans Group" of *Marmosa* by Tate (1933), who recognized eight of them as valid species. Subsequent authors have recognized as few as one to as many as 10 species in this group, which was first recognized as a valid genus in its currently accepted sense by Gardner and Creighton (1989). Although the current classification (Creighton and Gardner, 2008) is based on an impressive number of recent revisionary studies (Palma and Yates, 1998; Flores et al., 2000; Meynard et al., 2002; Palma et al., 2002; Solari, 2003; Braun et al., 2005; Carmignotto and Monfort, 2006), no study to date has included material from all of the species now regarded as valid.

Another notable aspect of most previous systematic analyses of *Thylamys* is an exclusive reliance either on molecular or morphological methods. Both approaches have unique advantages and limitations. Analyses

Fig. 1. *Thylamys pallidior* from Bahía Cracker (42°56′S, 64°20′W), Chubut, Argentina, photographed by Darío Podestá in January 2009.

based on DNA sequencing, for example, have the advantage of abundant character data, but sequence data can be difficult to interpret in the absence of phenotypic criteria linking gene trees to name-bearing types and other unsequenced material. Additionally, gene sequencing is relatively expensive, and the restricted availability of preserved tissue samples has hitherto limited molecular studies to treatments of no more than a few dozen individuals. By contrast, morphological analyses have the advantage of almost cost-free data collection and abundant material, but they are often hindered by a poverty of taxonomically informative characters.

Herein we combine both approaches by analyzing >100 mitochondrial gene sequences representing populations throughout the known distribution of *Thylamys*, including exemplars of all currently recognized species and most of the nominal taxa purported to be valid. We associated these sequence data with phenotypic character variation by examining morphological voucher material, and we assessed the taxonomic implications of our results by comparing voucher material with holotypes, neotypes, and other museum specimens.

Species Recognition Criteria

Despite a plethora of published species definitions (reviewed by deQueiroz, 1998), most evolutionary biologists agree that contemporaneous species should be genetically independent lineages. For a number of theoretical and practical reasons, mtDNA sequence monophyly and morphological diagnosability are now routinely used as joint criteria for species recognition by vertebrate systematists (Zamudio and Greene, 1997; Frost et al., 1998; Patton et al., 2000; Wiens and Penkrot, 2002). Because substitution rates and haplotype coalescence are, in general, much more rapid for mitochondrial than for nuclear genes (Moore, 1995; Palumbi and Cipriano, 1998), mitochondrial

sequence data are potentially more informative than nuclear DNA with regard to recent lineage formation. Morphological diagnosability, on the other hand, is important as a proxy for nuclear-gene divergence (Wiens and Penkrot, 2002) because it allows haplotype groups to be associated with appropriate clade names, and because it allows geographic ranges to be mapped without sequencing every specimen.

We recognize that some valid species might not be recovered as monophyletic haplotype groups due to incomplete lineage sorting of ancestral polymorphisms (Funk and Omland, 2003), and we are aware that some genetically isolated lineages might not have evolved diagnostic morphological characters (Baker and Bradley, 2006). However, given that speciation is a process, practical problems of delimitation will be encountered no matter what operational criteria are employed (Wiens and Penkrot, 2002; Sites and Marshall, 2003). In effect, our criteria are probably conservative, and in this respect our operationally defined species constitute hypotheses to be tested by future research.

Although a high degree of sequence divergence is not a necessary or sufficient criterion for species recognition (Ferguson, 2002; Baker and Bradley, 2006), it is relevant to note that congeneric didelphid species recognized on the basis of haplotype monophyly and morphological diagnosability (e.g., by Mustrangi and Patton, 1997; Patton and da Silva, 1997; Patton et al., 2000; Costa et al., 2003; Solari, 2007) differ by an average K2P-corrected pairwise divergence of about 10% at the cytochrome-*b* (CYTB) locus. This is (coincidentally) close to the threshold value for species delimitation suggested by Bradley and Baker (2001), but some didelphids that maintain unambiguously diagnostic morphological differences in sympatry—and so would be recognized as valid species by any current definition—have much less divergent CYTB sequences (e.g., 4% between *Philander mcilhennyi* and *P. opossum*; Patton and da Silva, 1997). Therefore, although we estimate pairwise sequence divergence for comparative purposes, we do not necessarily consider divergence values to be critical indicators of species status.

MATERIALS AND METHODS

Museum Collections

Morphological specimens and tissue samples used in the course of this study or cited in this report are preserved in the following collections: AMNH (American Museum of Natural History, New York), ANSP (Academy of Natural Sciences, Philadelphia), BMNH (Natural History Museum, London), CML (Colección de Mamíferos Lillo, Universidad Nacional de Tucumán, Tucumán), CNP (Centro Nacional Patagónico, Puerto Madryn), FMNH (Field Museum, Chicago), IADIZA (Instituto Argentino de Investigaciones en Zonas Áridas, Mendoza), MLP (Museo de La Plata, La Plata), MMNH (J.F. Bell Museum of Natural History, University of Minnesota, St. Paul), MNHN (Muséum National d'Histoire Naturelle, Paris), MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), MZUSP (Museu de Zoologia da Universidad do São Paulo, São Paulo), NMW (Naturhistorisches Museum Wien, Vienna), OMNH (Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman), TTU (Museum of Texas Tech University, Lubbock), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), USNM (National Museum of Natural History, Smithsonian Institution, Washington), UWBM (University of Washington Burke Museum, Seattle), ZMUC (Zoological Museum of the University of Copenhagen, Copenhagen), ZSM (Zoologische Staatssammlung München, Munich).

Taxon Sampling

We sequenced 131 specimens of *Thylamys* for this study (table 1), including representative material of all species currently recognized as valid by authors (Gardner, 2005; Creighton and Gardner, 2008; Teta et al., 2009). Within most species, multiple individuals from throughout the known geographic range were selected for sequencing in order to sample intraspecific genetic variation as completely as possible. In addition, we attempted to include representative material of all described nominal taxa (synonyms and

TABLE 1
List of Sequenced Specimens of *Thylamys*

Species[a]	Tissue[b]	Voucher	Locality[c]	Base pairs sequenced		
				CYTB	ND2	COX2
elegans	NK 27583	MSB 87097[d]	Chile: Coquimbo (88)	1149	1044	684
elegans	NK 95111	MSB 133104[d]	Chile: Metropolitana (89)	1149		
elegans	NK 96791	MSB 133097[d]	Chile: Metropolitana (90)	1149	1044	684
elegans	NK 27606	MSB 87098[d]	Chile: Valparaíso (92)	1149		
elegans	NK 96763	MSB 133095[d]	Chile: Valparaíso (93)	1149		
karimii	APC 1561	MZUSP 32094[e]	Brazil: Tocantins (87)	1149	1044	684
macrurus	APC 932	MZUSP 32094[d]	Brazil: Mato Grosso do Sul (86)	1149		
macrurus	NK 27536	MSB 70700[d]	Paraguay: Concepción (94)	1149	1044	684
pallidior	LTU 77	CNP 1919	Argentina: Buenos Aires (1)	1149		
pallidior	OCGR 3703	OMNH 29964[d]	Argentina: Catamarca (3)	1149	1044	684
pallidior	OCGR 7196	OMNH 34903[d]	Argentina: Catamarca (5)	1149		
pallidior	OCGR 3763	OMNH 32556[d]	Argentina: Catamarca (7)	1149		
pallidior	AC 47	MLP 24.X.01.3	Argentina: Córdoba (8)	1149		
pallidior	OCGR 3596	OMNH 29963[d]	Argentina: Jujuy (11)	1149		
pallidior	OCGR 2153	OMNH 29957[d]	Argentina: Jujuy (13)	1149		
pallidior	OCGR 7390	OMNH 34911[d]	Argentina: Jujuy (16)	1149		
pallidior	OCGR 4180	[uncataloged]	Argentina: La Rioja (19)	1149		
pallidior	OCGR 43	OMNH 23482[d]	Argentina: Mendoza (20)	1149	1044	684
pallidior	OCGR 230	OMNH 23480[d]	Argentina: Mendoza (21)	1149		
pallidior	UP 397	CNP 1921	Argentina: Neuquén (23)	1149		
pallidior	OCGR 3120	[uncataloged]	Argentina: Neuquén (24)	1149		
pallidior	OCGR 7279	OMNH 34908[d]	Argentina: Salta (25)	1149		
pallidior	OCGR 7294	OMNH 34909[d]	Argentina: Salta (25)	1149		
pallidior	OCGR 3957	OMNH 32559[d]	Argentina: Salta (26)	1149		
pallidior	OCGR 3996	OMNH 32544[d]	Argentina: Salta (28)	1149		
pallidior	OCGR 343	OMNH 23485[d]	Argentina: San Juan (30)	1149		
pallidior	OCGR 322	OMNH 32571[d]	Argentina: San Juan (31)	1149		
pallidior	OCGR 624	OMNH 23489[d]	Argentina: San Luis (32)	1149		
pallidior	OCGR 904	OMNH 23490[d]	Argentina: San Luis (33)	1149		
pallidior	OCGR 460	OMNH 23488[d]	Argentina: San Luis (34)	1149		
pallidior	NK 14721	MSB 57003[d]	Bolivia: Chuquisaca (45)	1149		
pallidior	NBH 76-97	FMNH 162495[d]	Bolivia: Tarija (73)	1149	1044	684
pallidior	NK 23533	MSB 87099[d]	Bolivia: Tarija (81)	1149	1044	684
pallidior	NK 96072	MSB 133108[d]	Chile: Tarapacá (91)	1149		
pallidior		MVZ 145531[d]	Peru: Arequipa (100)	1149		
pallidior		MVZ 173937[d]	Peru: Arequipa (99)	1149		
pallidior		MVZ 143696[d]	Peru: Tacna (104)	1149	283	178
pallidior		MVZ 115634[d]	Peru: Tacna (105)	1149		
pusillus	OCGR 1525	OMNH 23483[d]	Argentina: Catamarca (2)	1149	1044	684
pusillus	OCGR 3770	OMNH 32562[d]	Argentina: Catamarca (4)	1149		
pusillus		BMNH 98.8.19.12[d]	Argentina: Corrientes (9)	1149		
pusillus	LTU 539	CNP 1920[f]	Argentina: Entre Ríos (10)	1149	1044	684
pusillus		ZSM 1966/70[d]	Argentina: Misiones (22)	139		
pusillus	OCGR 4240	[uncataloged]	Argentina: Santiago del Estero (35)	1149		
pusillus	OCGR 1984	CML 3198[f]	Argentina: Santiago del Estero (36)	1149	1044	684
pusillus	NK 12574	MSB 55846[d]	Bolivia: Chuquisaca (44)	1149		
pusillus	NK 12539	AMNH 260025[d]	Bolivia: Santa Cruz (66)	1149	1044	684
pusillus	NK 25139	MSB 67016[d]	Bolivia: Tarija (76)	1149	1044	684
pusillus	NK 25141	AMNH 275440[d]	Bolivia: Tarija (77)	1149		
pusillus	TK 65612	TTU 109099[d]	Paraguay: Alto Paraguay (95)	1149		

TABLE 1
(Continued)

Species[a]	Tissue[b]	Voucher	Locality[c]	Base pairs sequenced		
				CYTB	ND2	COX2
pusillus	TK 66476	TTU 109052[d]	Paraguay: Boquerón (96)	1149	1044	684
sponsorius	OCGR 1363	OMNH 29965[d]	Argentina: Catamarca (6)	1149		
sponsorius	OCGR 3600	OMNH 29974[d]	Argentina: Jujuy (11)	1149		
sponsorius	OCGR 7432	OMNH 34534[d]	Argentina: Jujuy (15)	1149		
sponsorius	OCGR 2144	OMNH 29970[d]	Argentina: Jujuy (17)	1149		
sponsorius	OCGR 3986	OMNH 32548[d]	Argentina: Salta (27)	1149	1044	684
sponsorius	OCGR 3979	OMNH 32545[d]	Argentina: Salta (29)	1149	1044	684
sponsorius	OCGR 1346	OMNH 29967[d]	Argentina: Tucumán (37)	1149		
sponsorius	OCGR 1860	IADIZA 4009[g]	Argentina: Tucumán (38)	1149		
sponsorius	OCGR 2047	OMNH 32566[d]	Argentina: Tucumán (39)	1149		
sponsorius	OCGR 3448	OMNH 29977[d]	Argentina: Tucumán (42)	1149		
sponsorius	OCGR 3929	OMNH 32553[d]	Argentina: Tucumán (43)	1149		
sponsorius		FMNH 29170[d]	Bolivia: Tarija (71)	812[h]		
sponsorius		UMMZ 155836[d]	Bolivia: Tarija (71)	609[h]		
sponsorius	BDP 3345	FMNH 162505[d]	Bolivia: Tarija (72)	1149	1044	684
sponsorius	NK 23762	MSB 67014[d]	Bolivia: Tarija (74)	863		
sponsorius	NK 23763	MSB 67015[d]	Bolivia: Tarija (74)	1149		
sponsorius	NK 23901	AMNH 275437[d]	Bolivia: Tarija (75)	1149		
sponsorius	NK 23903	MSB 67010[d]	Bolivia: Tarija (75)	1149		
sponsorius	NK 23904	MSB 67012[d]	Bolivia: Tarija (75)	1149		
sponsorius	NK 23647	MSB 140295	Bolivia: Tarija (78)	849		
sponsorius	BDP 3309	FMNH 162507[d]	Bolivia: Tarija (79)	1149		
sponsorius	NK 23874	[uncataloged]	Bolivia: Tarija (80)	863		
sponsorius	NK 23899	[uncataloged]	Bolivia: Tarija (80)	863		
sponsorius	NK 23719	MSB 67009[d]	Bolivia: Tarija (83)	863		
tatei		MVZ 135504[d]	Peru: Ancash (97)	1149	283	178
tatei		MVZ 135503[d]	Peru: Ancash (97)	1038[h]		
velutinus		OMNH 37216[d]	Brazil: Distrito Federal (84)	1149	283	684
velutinus		OMNH 22284[d]	Brazil: Distrito Federal (85)	1149	283	
venustus	OCGR 2071	OMNH 29952[d]	Argentina: Jujuy (12)	1149		
venustus		AMNH 185323[d]	Argentina: Jujuy (14)	1008		
venustus		AMNH 186948[d]	Argentina: Jujuy (18)	1008		
venustus	OCGR 3553	OMNH 29976[d]	Argentina: Tucumán (40)	1149		
venustus	OCGR 1007	OMNH 29966[d]	Argentina: Tucumán (41)	1149	1044	684
venustus	NK 12575	AMNH 261245[d]	Bolivia: Chuquisaca (44)	1149		
venustus	NK 21367	MSB 63261[d]	Bolivia: Chuquisaca (46)	1149		
venustus	NK 21368	MSB 63262[d]	Bolivia: Chuquisaca (46)	1149		
venustus	NK 21655	MSB 63267[d]	Bolivia: Chuquisaca (47)	1149		
venustus	NK 21664	MSB 63268[d]	Bolivia: Chuquisaca (47)	1149		
venustus	NK 21515	AMNH 263558[d]	Bolivia: Chuquisaca (48)	1149		
venustus	NK 21516	MSB 63269[d]	Bolivia: Chuquisaca (48)	1149		
venustus	NK 10879	[uncataloged]	Bolivia: Chuquisaca (49)	1149		
venustus	NK 12637	AMNH 261254[d]	Bolivia: Chuquisaca (49)	1149	1044	684
venustus	NK 12638	AMNH 261260[d]	Bolivia: Chuquisaca (49)	1149		
venustus	NK 12642	AMNH 261255	Bolivia: Chuquisaca (49)	1149		
venustus	NK 12552	AMNH 261264	Bolivia: Chuquisaca (50)	1149		
venustus	NK 21815	MSB 63264[d]	Bolivia: Chuquisaca (51)	1149		
venustus	NK 21556	AMNH 263556[d]	Bolivia: Chuquisaca (52)	1149	1044	684
venustus	NK 21546	AMNH 263555[d]	Bolivia: Chuquisaca (53)	1149		
venustus	NK 21620	MSB 63272[d]	Bolivia: Chuquisaca (54)	1149		
venustus	NK 21621	MSB 63265[d]	Bolivia: Chuquisaca (54)	1149		
venustus	NK 21622	MSB 63273[d]	Bolivia: Chuquisaca (54)	1149		

TABLE 1
(Continued)

Species[a]	Tissue[b]	Voucher	Locality[c]	Base pairs sequenced		
				CYTB	ND2	COX2
venustus	NK 30425	AMNH 275427[d]	Bolivia: Cochabamba (55)	1149		
venustus	NK 25027	MSB 87109[d]	Bolivia: Cochabamba (56)	1149		
venustus	NK 30437	MSB 87100[d]	Bolivia: Cochabamba (56)	1149	1044	684
venustus	NK 30479	AMNH 275429[d]	Bolivia: Cochabamba (56)	1149		
venustus	NBH 2020	[uncataloged][d]	Bolivia: Cochabamba (57)	1149	1044	684
venustus	NK 22844	AMNH 275428[d]	Bolivia: Cochabamba (58)	1149	1044	684
venustus	NK 22845	MSB 67001[d]	Bolivia: Cochabamba (58)	950[h]		
venustus		AMNH 248704[d]	Bolivia: La Paz (59)	807		
venustus		AMNH 248705[d]	Bolivia: La Paz (59)	1008		
venustus	NK 21237	MSB 63260[d]	Bolivia: Santa Cruz (60)	1149		
venustus	NK 12114	AMNH 260030[d]	Bolivia: Santa Cruz (61)	1149		
venustus	NK 22815	MSB 87106[d]	Bolivia: Santa Cruz (62)	1149		
venustus	NK 22811	[uncataloged]	Bolivia: Santa Cruz (63)	1149		
venustus	NK 22813	MSB 87107[d]	Bolivia: Santa Cruz (63)	1149		
venustus	NK 22946	MSB 67003[d]	Bolivia: Santa Cruz (64)	1149		
venustus	NK 22949	[uncataloged]	Bolivia: Santa Cruz (65)	1149		
venustus	NK 22952	AMNH 275433[d]	Bolivia: Santa Cruz (65)	1149	1044	684
venustus	NK 23023	MSB 67005[d]	Bolivia: Santa Cruz (67)	1149		
venustus	NK 22986	MSB 67004[d]	Bolivia: Santa Cruz (68)	1149		
venustus	NK 23347	MSB 67007[d]	Bolivia: Tarija (69)	1149		
venustus	NK 23992	MSB 67392[d]	Bolivia: Tarija (70)	1149		
venustus	NK 23730	[uncataloged]	Bolivia: Tarija (74)	1149		
venustus	NK 23392	MSB 67008[d]	Bolivia: Tarija (82)	1149		
venustus	NK 30760	MSB 140320	Bolivia: Tarija (82)	1149		
venustus	NK 30761	MSB 140321	Bolivia: Tarija (82)	1149		
sp.		MVZ 116614[d]	Peru: Arequipa (98)	1149		
sp.		MVZ 137896[d]	Peru: Ayacucho (101)	1149		
sp.		MVZ 119913[d]	Peru: Lima (102)	493[h]		
sp.		MVZ 137585[d]	Peru: Lima (103)	866[h]		

[a]As recognized in this report.
[b]Sequences amplified from skins lack entries in this column.
[c]Numbers in parentheses refer to entries in the Gazetteer (appendix 1).
[d]Examined by us.
[e]Examined by Ana P. Carmignotto (personal commun.).
[f]Examined by Teta et al. (2009).
[g]Examined by Flores et al. (2007).
[h]Cytochrome-*b* sequence data is noncontiguous for this individual.

"subspecies") to resolve longstanding nomenclatural issues.

Outgroup taxa were selected based on the phylogenetic results of Voss and Jansa (2009). These include *Lestodelphys halli* (the sister taxon of *Thylamys*) and exemplar species of three other thylamyine genera (*Cryptonanus*, *Gracilinanus*, *Marmosops*; table 2). On the assumption of thylamyine monophyly, sequences downloaded from GenBank for the marmosine species *Monodelphis domestica* (complete mitochondrial genome accession number AJ508398) were used to root all of our trees.

DNA Extraction and Gene Sequencing

For the majority of specimens, DNA was extracted using a Qiagen DNA Minikit (Qiagen Inc.) from kidney, liver, or muscle tissue that had been preserved in ethanol or frozen in the field. However, we also extracted DNA from pieces of dried tissue snipped from skins or scraped from skeletal

TABLE 2
List of Sequenced Specimens of Outgroup Taxa

Species	Tissue	Voucher	Base pairs sequenced		
			CYTB	ND2	COX2
Cryptonanus unduaviensis	NK 14234	AMNH 262401	973	1038	684
Gracilinanus emiliae	DWF 413	MUSM 15292	943	1044	684
Lestodelphys halli	CNP 889	CNP 889	1149	1044	684
Lestodelphys halli	PNG 1398	CNP 1741	1149	1044	
Marmosops impavidus	NK 14140	MSB 57002	1107	1039	684

specimens. All extractions and subsequent sequence amplifications for dried tissues were conducted in a UV-sterilized hood to avoid contamination with foreign DNA. To further minimize the risk of contamination, all procedures conducted prior to amplification were conducted in a laboratory in which amplified mammalian DNA has never been present. Most of the museum specimens from which such material was removed are decades old and have been handled extensively, so it was necessary to thoroughly wash the samples in order to remove foreign DNA and potential PCR inhibitors. First, we washed whole pieces of the dried tissue in 800 μL of 100% ethanol by vortexing the sample for one minute and letting it rest overnight. The following day, we removed the liquid, resuspended the tissue in 100% ethanol, vortexed the sample for an additional minute, and then immediately repeated the same wash. We repeated a similar set of three washes (one overnight, then two for one minute) using 70% ethanol and then, finally, using water, for a total of nine washes per sample. We extracted DNA using a Qiagen DNA Minikit (Qiagen Inc.) after the washed tissue samples were digested for 48 hours in a solution of tissue lysis buffer and as much proteinase K as was necessary to completely digest the sample, typically 30–40 μL.

We amplified and sequenced three mitochondrial protein-coding genes for this study: cytochrome *b* (CYTB, ~1.1 kb), cytochrome *c* oxidase subunit II (COX2, ~0.7 kb), and NADH dehydrogenase 2 (ND2, ~1.0 kb). We sequenced CYTB for all individuals (131 ingroup, five outgroup), whereas COX2 and ND2 were sequenced for all of the outgroup taxa and for a subset of 28 individuals representing all major CYTB haplogroups (see Results). For frozen and ethanol-preserved samples, amplification of CYTB and ND2 required two steps: one round to amplify the whole gene, followed by a second round of amplification using internal primers, which, depending on the gene and taxon, yielded two or three appropriately sized fragments for sequencing. The targeted COX2 sequence was short enough to amplify and sequence in one step. Museum specimens typically yielded highly degraded DNA, which necessitated the use of dozens of specific primer pairs that amplified 150–300 bp fragments. All primer sequences can be found in appendix 2.

We cleaned PCR products of excess primers and unincorporated nucleotides prior to sequencing using Exonuclease I and Shrimp Alkaline Phosphatase (Hanke and Wink, 1994). We sequenced these products in both directions on an ABI 3730 automated sequencer (Applied Biosystems Inc.) using amplification primers and dye-terminator chemistry (BigDye ver. 3.1 Cycle Sequencing Kit, Applied Biosystems Inc., Foster City, California). We used Sequencher 4.7 (GeneCodes Inc., Ann Arbor, Michigan) to compile and edit the sequences and MEGA 4.0 (Tamura et al., 2007) to determine sequence characteristics and genetic distances. All sequences have been deposited in GenBank

(CYTB: HM583364–HM583499; COX2: HM583500–HM583532; ND2: HM583533–HM583566).

Phylogenetic Analyses

DNA sequences for each gene were aligned with reference to translated amino acid sequences; no insertions or deletions were necessary. We performed phylogenetic analyses using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Analyses were conducted with four datasets: one for each of the three genes alone and one that includes the three genes in combination. The CYTB dataset included multiple sequences for most of the species, ranging from one representative individual (*T. karimii*) to 48 (*T. venustus*). In contrast, the ND2 and COX2 datasets include no more than three sequences from any given haplogroup (see Results). Because of the disparity in size among the single-gene datasets, the combined-gene dataset includes CYTB sequences from only those individuals for which we had also sequenced ND2 and COX2.

MAXIMUM PARSIMONY AND MAXIMUM LIKELIHOOD ANALYSES: For each of the four datasets, we implemented MP analyses in PAUP* 4.0 (Swofford, 2002) using a heuristic search strategy with TBR branch swapping, 10 random-addition replicates, and with all characters unordered and equally weighted. We assessed nodal support using 5000 bootstrap pseudoreplicates with TBR branch swapping and 10 random-addition replicates. For the CYTB dataset, we first pruned out identical sequences in order to maximize computational efficiency.

We conducted ML analyses of each of the four datasets in GARLI ver. 0.96 (Zwickl, 2006) by specifying the best-fit model for each dataset as determined in MrModelTest 2.3 (Nylander, 2004) and allowing the model parameters to be estimated from the data. We did not alter the default parameters used in the program's genetic algorithm, and we set the analyses to automatically terminate after 20,000 generations with no significant change in the log-likelihood score. In order to ensure that the program had arrived at a stable log-likelihood estimate, we repeated each search five times and report only the estimate with the highest log-likelihood. We measured nodal support using 500 bootstrap replicates and the same settings used in the individual ML analyses.

DATA PARTITIONING IN A BAYESIAN FRAMEWORK: Combining data from multiple genes and treating each codon position identically assumes that each site within the dataset evolves under the same nucleotide substitution model. If this assumption is invalid, as is often the case, the dataset can be partitioned into independent units (e.g., Bull et al., 1993; Nylander et al., 2004) in order to avoid misleading results (Brown and Lemmon, 2007). For each of the four datasets, we evaluated the relative fit of different data-partitioning strategies in a Bayesian framework. For the three single-gene datasets, we tested whether a three-partition (by codon position) model fit the data significantly better that a single (unpartitioned) model. For the combined-gene dataset, we evaluated the relative fit of four partitioning strategies: (1) a single partition for all genes in combination (combined: unpartitioned); (2) three partitions, one for each of the three genes (by gene); (3) three partitions, one for each of the codon positions across all genes (combined: by codon position); and (4) nine partitions, one for each codon position for each of the three genes (by gene by codon position).

Several statistical approaches have been suggested in the literature for evaluating the relative fit of different partitioning schemes, including Bayes factors (Kass and Raftery, 1995), the Akaike information criterion (AIC; Akaike, 1974), and the Bayesian information criterion (BIC; Schwarz, 1978). Although Bayes factors have been shown to be reasonably effective tools for choosing among partitioning schemes (Brown and Lemmon, 2007), the number of parameters contained in alternative models is not explicitly incorporated into the calculation of Bayes factors. The AIC and BIC both apply penalties to the addition of parameters, mitigating the problems associated with overparameterization (McGuire et al., 2007). Therefore, to account for potential overparameterization, we only ranked partitioning strategies using the AIC and BIC.

To implement this approach, we obtained log-likelihood scores and model parameter values for each of the partitioning strategies described above for the four datasets using BI as implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). We first determined the best-fitting nucleotide substitution model for each individual partition using the AIC as implemented in MrModeltest. We specified the appropriate model for each partition in MrBayes and, for strategies with more than one partition, we unlinked all substitution parameters across partitions. We estimated branch lengths proportionally to each partition and allowed the substitution rate to vary across each partition by setting the rate prior option to "variable." We ran two independent replicates of the Metropolis-Coupled Markov Chain Monte Carlo analysis for 5×10^6 generations, sampling every 100th generation, with one cold chain and three incrementally heated chains.

Once these runs were completed, we examined a plot of the log-likelihood scores per generation using Tracer 1.4 (Rambaut and Drummond, 2007) to determine the appropriate number of generations to discard as burn-in. For all strategies and datasets, we discarded the first 500,000 generations (5,000 saved samples)—well after the log-likelihood scores stabilized—and used the remaining 45,000 samples to estimate mean log-likelihood, nodal posterior probability (BPP) values, mean branch lengths, and other parameters. In order to compare the results of different partitioning strategies, we calculated the harmonic mean log-likelihood (HML) across all parameters for each strategy in Tracer. We then used the HML values to calculate the AIC and BIC scores according to the methods of McGuire et al. (2007).

TOPOLOGY TESTS: Previously published molecular and morphological research on *Thylamys* has produced several phylogenies that differ from ours. In order to evaluate these alternative hypotheses, we conducted topology tests using Shimodaira-Hasegawa (SH) likelihood-ratio tests (Shimodaira and Hasegawa, 1999). First, an ML analysis was performed in GARLI following the same protocol described above, except that constraint trees were used to infer the best tree that conformed to the alternative hypothesis in question. We then implemented the SH test in PAUP* using 1000 resampling estimated log likelihoods (RELL) replicates to compare the constrained ML tree to the best ML tree from the above analysis, allowing the program to estimate all parameters.

PARSIMONY ANCESTRAL STATE RECONSTRUCTION: Species and haplogroups that comprise the Elegans Group (see Results) occur on both the eastern and western sides of the Andes. We used the combined-gene ML topology to reconstruct the ancestral distributions of Elegans Group lineages relative to the Andes. Tips were coded as occurring east of the Andes (cis-Andean), west of the Andes (trans-Andean), or both (ambiguous). We optimized ancestral areas on the topology using the parsimony criterion for ancestral state optimization of unordered characters as implemented in MacClade 4.08 (Maddison and Maddison, 2000).

Morphology

We recorded measurement data and scored qualitative morphological characters from voucher specimens in order to assess the phenotypic distinctness of mitochondrial haplotype clades and to provide a basis for comparisons with holotypes and other unsequenced material. Except as noted otherwise below, all analyzed character data were obtained from adult specimens as determined by dental criteria. Specimens were judged to be *juvenile* if dP3 was still in place, *subadult* if dP3 had been shed but P3 was still incompletely erupted, and *adult* if the permanent dentition was complete.

MEASUREMENT DATA: We transcribed total length (nose to fleshy tail tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), and length of ear (from notch, Ear), from specimen labels or field notes. Additionally, we remeasured HF to check the accuracy of values recorded by the collector, and we used our values whenever large discrepancies were found. All external mea-

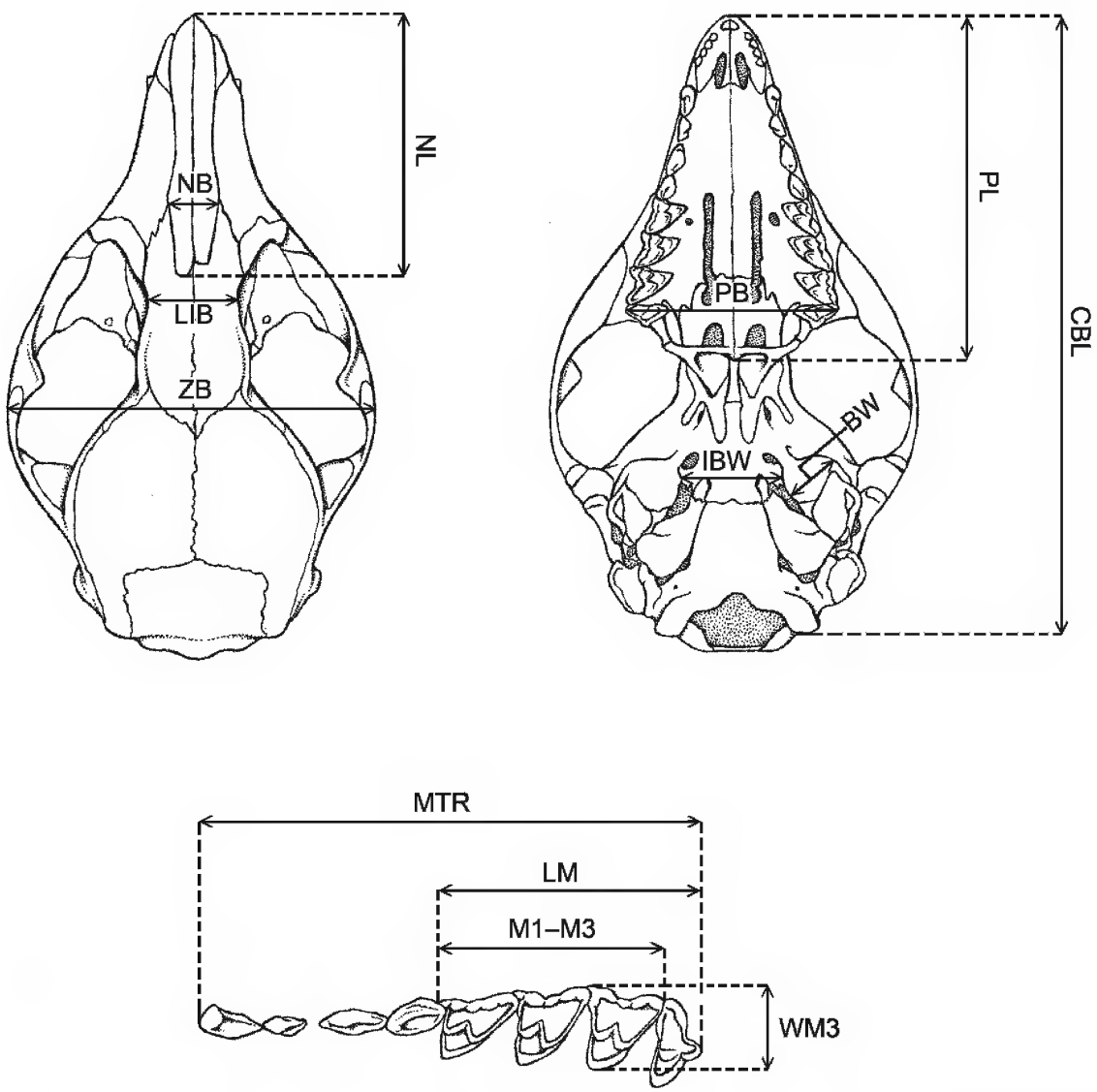

Fig. 2. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Thylamys pusillus*, showing the anatomical limits of 13 craniodental measurements defined in the text.

surements are reported to the nearest millimeter (mm).

Craniodental measurements were taken with digital calipers as skulls were viewed under low (6–12×) magnification and recorded to the nearest 0.01 mm, but measurement values reported herein are rounded to the nearest 0.1 mm. The following dimensions were measured as illustrated in figure 2:

Condylo-basal length (CBL): Measured from the occipital condyles to the anteriormost point of the premaxillae.

Nasal breadth (NB): Measured across the triple-point sutures of the nasal, frontal, and maxillary bones on each side.

Least interorbital breadth (LIB): Measured at the narrowest point across the frontals between the orbits.

Zygomatic breadth (ZB): Measured at the widest point across both zygomatic arches.

Palatal length (PL): Measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present).

Palatal breadth (PB): Measured across the labial margins of the upper fourth molar (M4) crowns, at or near the stylar A position.

Maxillary toothrow length (MTR): Measured from the anterior margin of the upper canine (C1) to the posterior margin of ipsilateral M4.

Length of molars (LM): Measured from the anteriormost labial margin of M1 to the posteriormost point on ipsilateral M4.

Length of M1–M3 (M1–M3): Measured from the anteriormost labial margin of M1 to the posteriormost point on ipsilateral M3.

Width of M3 (WM3): Measured from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

In addition, we took two other measurements to record taxonomic variation in bullar inflation remarked by authors and confirmed by our own visual comparisons of skulls:

Bullar width (BW): Measured from the glenoid fossa across the inflated, bubblelike part of the alisphenoid tympanic process to its posteromedial extremity.

Interbullar width (IBW): The least distance between the medial surfaces of the left and right bullae.

QUALITATIVE CHARACTERS: We examined skins, skulls, and fluid-preserved specimens for taxonomic variation in qualitative morphological characters. Surveyed characters included those previously described in the didelphid taxonomic literature (e.g., Tate, 1933; Flores et al., 2000; Solari, 2003; Voss and Jansa, 2003; Carmignotto and Monfort, 2006) and others newly reported herein. Nomenclature used to describe observed variation in integumental, osteological, and dental features follows standard anatomical usage as reviewed by Voss and Jansa (2009).

MOLECULAR RESULTS

Sequence Characteristics

Our cytochrome-*b* dataset comprises aligned sequence data for 131 ingroup individuals. In 115 cases, we obtained sequence from the complete CYTB gene (1149 bp); the remaining 16 CYTB sequences range in length from 139 to 1038 bp.[1] In addition, we sequenced 283–1044 bp of the ND2 gene and 178–684 bp of the COX2 gene from 28 individuals representing all but one of the major lineages recovered from analyses of the CYTB dataset. We combined the resulting sequences with CYTB sequences from the same individuals to obtain a concatenated, three-gene alignment that was 2877 bp long. We were unable to amplify ND2 or COX2 from any of the undescribed Peruvian specimens (*Thylamys* sp.; see Results) and therefore scored those genes as missing data for the only example of the undescribed Peruvian form included in our combined-gene analysis.

Nucleotide-substitution characteristics were estimated for each gene using the best-fitting model. For all three genes, a general-time-reversible (GTR) model best fits the data (table 3). Each model also incorporates an among-site rate heterogeneity parameter (α) as approximated by the gamma distribution and a proportion of invariant-sites parameter (p_{inv}). Base-frequency parameter estimates (πA, πC, πG, πT) demonstrate that all three genes are AT-rich with a marked paucity of guanine residues, similar to other estimates of the base composition of mammalian mitochondrial DNA (Irwin et al., 1991; Patton et al., 1996). None of the three genes showed any departure from base-compositional stationarity among individuals (CYTB: $\chi^2 = 86.19$ [$df = 405$], $P = 1.00$; ND2: $\chi^2 = 51.45$ [$df = 69$], $P = 0.94$; COX2: $\chi^2 = 14.59$ [$df = 78$], $P = 1.00$).

Phylogenetic Analyses

For each of the four datasets, phylogenetic relationships were inferred using MP, ML,

[1] Six CYTB sequences (noted in table 1) include unsequenced regions ranging in length from 2 to 635 bp long because one or more internal fragments could not be amplified, yielding noncontiguous data. To ensure that each non-overlapping fragment for a given individual was from the same locus—and not from a nuclear pseudogene or contaminant organism—we analyzed each fragment separately in a single ML run using the same parameters described above. In all cases, each fragment clustered near the other fragment(s) ostensibly derived from the same locus, consistent with the hypothesis that all non-contiguous fragments were derived from a single locus. Therefore, we treated the unsequenced regions in question as missing data in all of the analyses.

TABLE 3
Results of Maximum-likelihood Model Fitting with Single-gene Datasets

	CYTB[a]	CYTB[b]	ND2	COX2
No. sequences[c]	137	35	34	32
Model	GTR + I + Γ	GTR + I + Γ	GTR + I + Γ	GTR + I + Γ
πA	0.35	0.35	0.37	0.36
πC	0.28	0.28	0.30	0.22
πG	0.05	0.06	0.05	0.11
πT	0.32	0.31	0.29	0.31
rAC	0.82	1.16	0.34	1.04
rAG	39.2	41.11	11.4	18.94
rAT	1.81	2.35	0.63	1.93
rCG	1.47	0.77	0.27	0.38
rCT	18.9	23.43	4.58	21.07
α	1.79	1.93	1.28	1.15
p_{inv}	0.54	0.55	0.36	0.57
Ln-likelihood[d]	−10723.24	−8867.26	−8867.43	−4341.90

[a]Full taxon sampling.
[b]Subsample of specimens for which ND2 and COX2 sequences are also available.
[c]Including outgroups.
[d]Of best tree.

and BI analyses. Maximum parsimony analysis of each dataset resulted in well-resolved strict consensus trees (table 4). Because we recovered the same species-level clades in all analyses of each dataset, we show only the ML phylogenies in this report and superimpose nodal support values from each analysis on that tree. For MP and ML analyses, support for a node is considered strong if that node receives bootstrap values 75% or greater, moderate for values between 50% and 75%, and weak for values of 50% or less. For BI, nodes are considered strongly supported for BPP values greater than or equal to 0.95 and weakly supported for values less than 0.95.

Individual BI analyses were conducted for each data-partitioning strategy and results were ranked by the AIC and BIC according to their fit (table 5). For each dataset, only

TABLE 4
Results of Parsimony Analyses of Molecular Datasets

	CYTB[a] (Full taxon sampling)	CYTB (Subsample)	ND2	COX2	Concatenated
Ingroup sequences	100	29	28	27	29
Outgroup sequences	6	6	6	5	6
Aligned sites	1149	1149	1044	684	2877
Variable sites	501	489	590	257	1336
% variable sites	43.6	42.6	56.5	37.6	46.5
Informative sites	456	431	493	210	1134
Minimum-length trees	324	1	1	6	2
Length of best tree(s)	2022	1767	1819	820	4431
Consistency Index	0.35	0.40	0.48	0.44	0.44
Retention Index	0.65	0.67	0.70	0.65	0.68
Resolved nodes (%)[b]	72 (72.7)	28 (100)	27 (100)	24 (92.3)	28 (100)

[a]Only nonidentical, complete sequences were used to calculate statistics for CYTB.
[b]Among ingroup sequences in strict consensus of minimum-length trees.

TABLE 5
Test of Alternative Partitioning Strategies

Dataset	Partition Name (No. data partitions)	No. Parameters	Harmonic-Mean Log-Likelihood	AIC Score (rank)	BIC Score (rank)
CYTB[a]	Unpartitioned (1)	12	−11051.301	22126.877 (2)	24096.803 (2)
	By codon (3)*	39	−10508.431	21097.675 (1)	23201.323 (1)
ND2	Unpartitioned (1)	12	−8954.722	17933.747 (2)	18458.483 (2)
	By codon (3)*	39	−8593.582	17268.275 (1)	17923.849 (1)
COX2	Unpartitioned (1)*	12	−4433.421	8891.307 (1)	9369.495 (1)
	By codon (3)	19[b]	−4563.162	9209.169 (2)	9805.2316 (2)
Combined	Unpartitioned (1)	12	−22282.984	44590.077 (4)	45195.164 (3)
	By gene (3)	39	−22201.804	44482.708 (3)	45247.845 (4)
	By codon (3)*	39	−21146.311	42371.722 (1)	43136.859 (1)
	By gene by codon (9)	91[b]	−21578.187	43344.386 (2)	44414.766 (2)

*Best-fit partitioning strategy for a given dataset.
[a]Dataset with full taxon sampling (137 individuals).
[b]Best-fit models for each COX2 codon position are as follows: SYM+I+Γ (first positions), HKY (second positions), and HKY+I+Γ (third positions).

the results from the best-fitting strategy are presented below, and in all of those cases, a GTR+I+Γ nucleotide-substitution model was found to fit each partition best. For the CYTB and ND2 single-gene datasets, the "by codon" partitioning scheme fit the data better than the unpartitioned scheme. The unpartitioned scheme fit the data best for the single-gene COX2 dataset. For the combined-gene dataset, the partitioning strategy that pooled codon positions across the three genes fit the data best.

SPECIES LIMITS AND PHYLOGEOGRAPHIC STRUCTURE: Nine of the monophyletic groups of *Thylamys* that we recovered by analyzing cytochrome-*b* sequence data appear to represent valid species (fig. 3, table 6). In order to simplify the presentation of these results, we anticipate our taxonomic conclusions by using Latin binomials for reciprocally monophyletic groups of sequences obtained from morphologically differentiated series of voucher specimens, and we use alphabetical designations (A, B, C) for reciprocally monophyletic groups of apparently conspecific sequences ("haplogroups"). The morphological basis for assigning names to clades is explained in a separate section of this report (see Taxonomy, below).

The first two lineages to branch within *Thylamys* are Brazilian endemic species—*Thylamys karimii* and *T. velutinus* (both sensu Carmignotto and Monfort, 2006)—that are represented in these data by only one and two individual(s), respectively. Also sparsely sampled is *T. macrurus*, a species that inhabits eastern Paraguay and the adjoining Brazilian state of Mato Grosso do Sul (Carmignotto and Monfort, 2006; Voss et al., 2009). Three clades recovered by all analyses of the CYTB data incorporate the remaining species: the Elegans Group (node 1), *Thylamys pusillus* (node 2), and the Venustus Group (node 3).

The Elegans Group (fig. 4) consists of at least three species that collectively range from Patagonia to Peru (fig. 5). *Thylamys elegans,* a name that we apply in the restricted sense of Meynard et al. (2002) and Solari (2003), is represented in these data by five sequences from central Chile that form a robustly supported monophyletic group in all of our analyses. Despite the fact that *T. elegans* has a geographically restricted distribution, the uncorrected average sequence divergence among these haplotypes is moderately high, about 2.5% (table 6). Sequence divergence across the basal split in this species is somewhat higher (3.8%), but it is far less than the 8.6% difference that Meynard et al. (2002) reported among their Chilean specimens. Although we are unable to account for this discrepancy (we sequenced only one of the specimens that Meynard et al. included in their study, NK 27583), we note that Braun

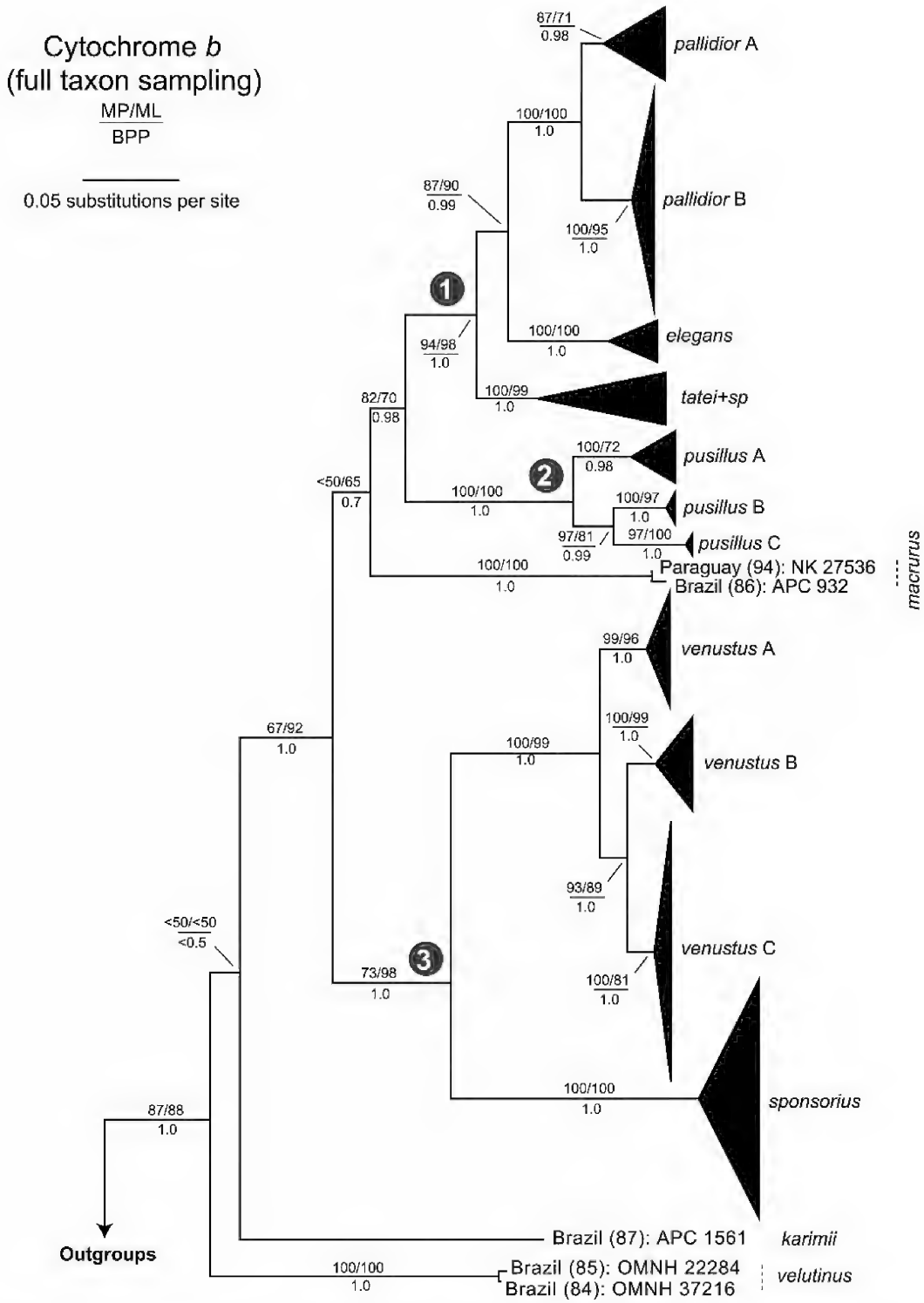

Fig. 3. The tree based on ML analysis of cytochrome-*b* sequences for 131 ingroup terminals and six individuals representing five outgroup genera (GTR + I + Γ, ln-likelihood = −10723.24). Maximum

TABLE 6
Uncorrected Cytochrome-*b* p-Distances (scaled as percent sequence divergence; below diagonal), K2P-Corrected Distances (above diagonal), and Intraspecific Distances (diagonal)[a]

	1	2	3	4	5	6	7	8	9	10
1. *T. elegans*	**2.5**	17.1	15.3	10.3	14.8	10.6	16.5	10.7	17.7	16.0
2. *T. karimii*	14.9	-	15.7	16.3	16.6	15.1	18.7	15.5	15.6	18.4
3. *T. macrurus*	13.5	13.9	**0.8**	15.2	15.7	14.6	15.7	14.7	18.5	15.9
4. *T. pallidior*	9.4	14.3	13.4	**2.7**	13.7	10.9	18.2	10.6	16.3	16.3
5. *T. pusillus*	13.1	14.6	13.8	12.2	**5.1**	13.4	17.9	13.7	18.0	16.7
6. *T.* sp.	9.7	13.4	13.0	9.9	12.1	**2.9**	17.2	6.8	16.9	15.9
7. *T. sponsorius*	14.4	16.1	13.8	15.6	15.4	14.9	**1.8**	17.7	18.8	14.1
8. *T. tatei*	9.8	13.8	13.1	9.7	12.3	6.4	15.3	**0.1**	16.8	16.1
9. *T. velutinus*	15.4	13.7	16.0	14.3	15.6	14.8	16.1	14.7	**0.2**	15.9
10. *T. venustus*	14.1	15.9	14.0	14.3	14.6	14.1	12.5	14.2	14.0	**3.2**

[a]Off-diagonal table entries are mean pairwise distances among all sequences assigned to row and column taxa. Intraspecific distances are averaged over all pairwise comparisons of conspecific sequences; mean differences across the basal split within species (as reported in the text) are generally higher. K2P-corrected values were computed for comparison with previous studies of didelphid CYTB sequence variation (e.g., Patton et al., 1996, 2000), most of which used this model-based distance metric.

et al. (2005) reanalyzed Meynard et al.'s *T. elegans* sequences and obtained an average divergence value of 1.94%.

A second species in the Elegans Group is *Thylamys pallidior,* a name that we apply to specimens from southern Peru, northern Chile, the Bolivian altiplano, and Argentina. The monophyly of *T. pallidior* is robustly supported in all of our analyses of CYTB sequence data, but average uncorrected sequence divergence is moderately high (5.0%) across the basal split in this species, which separates two reciprocally monophyletic haplogroups. The northern haplogroup (*pallidior* A) occurs in Peru, Bolivia, and northern Chile and comprises two well supported subgroups differing by a net uncorrected p-distance of 2.5%. The southern haplogroup (*pallidior* B), although restricted to Argentina, is widely distributed in that country, where it occurs from high elevations (> 4000 m) in the Andes to near sea level in the Pampas; despite this impressive ecogeographic range, genetic diversity within *pallidior* B is low (about 1.0%) and there is little apparent phylogeographic structure among the 22 member sequences that we analyzed.

The third species that we recognize in the Elegans Group is *Thylamys tatei*, represented by two individuals from west-central Peru (Ancash) that differ in sequence at only one nucleotide position. Interestingly, this genetically and morphologically distinctive taxon is part of an unresolved trichotomy with two other divergent lineages, also from western Peru, that may represent undescribed species (E. Palma, personal commun.).

Thylamys pusillus, a name that we apply to three allopatric haplogroups (fig. 6), is a lowland species from the tropical and subtropical dry forests and savannas of southeastern Bolivia, western Paraguay, and northern Argentina (fig. 7). The three haplogroups recovered in our analysis correspond to those recently reported by Teta et al. (2009), who recognized them as valid

←

parsimony (MP) and maximum likelihood (ML) bootstrap values and Bayesian posterior probabilities (BPP) are indicated at all nodes. Individual specimens of *Thylamys macrurus*, *T. karimii*, and *T. velutinus* are labeled with country of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 1). Other species (and haplogroups) are cartooned with black triangles, the breadth (vertical dimension) of which is proportional to the number of individuals sampled for each clade, and the length (horizontal extent) of which is proportional to genetic diversity within each clade. Clades numbered in gray circles are presented as subtrees in figures 4, 6, and 8.

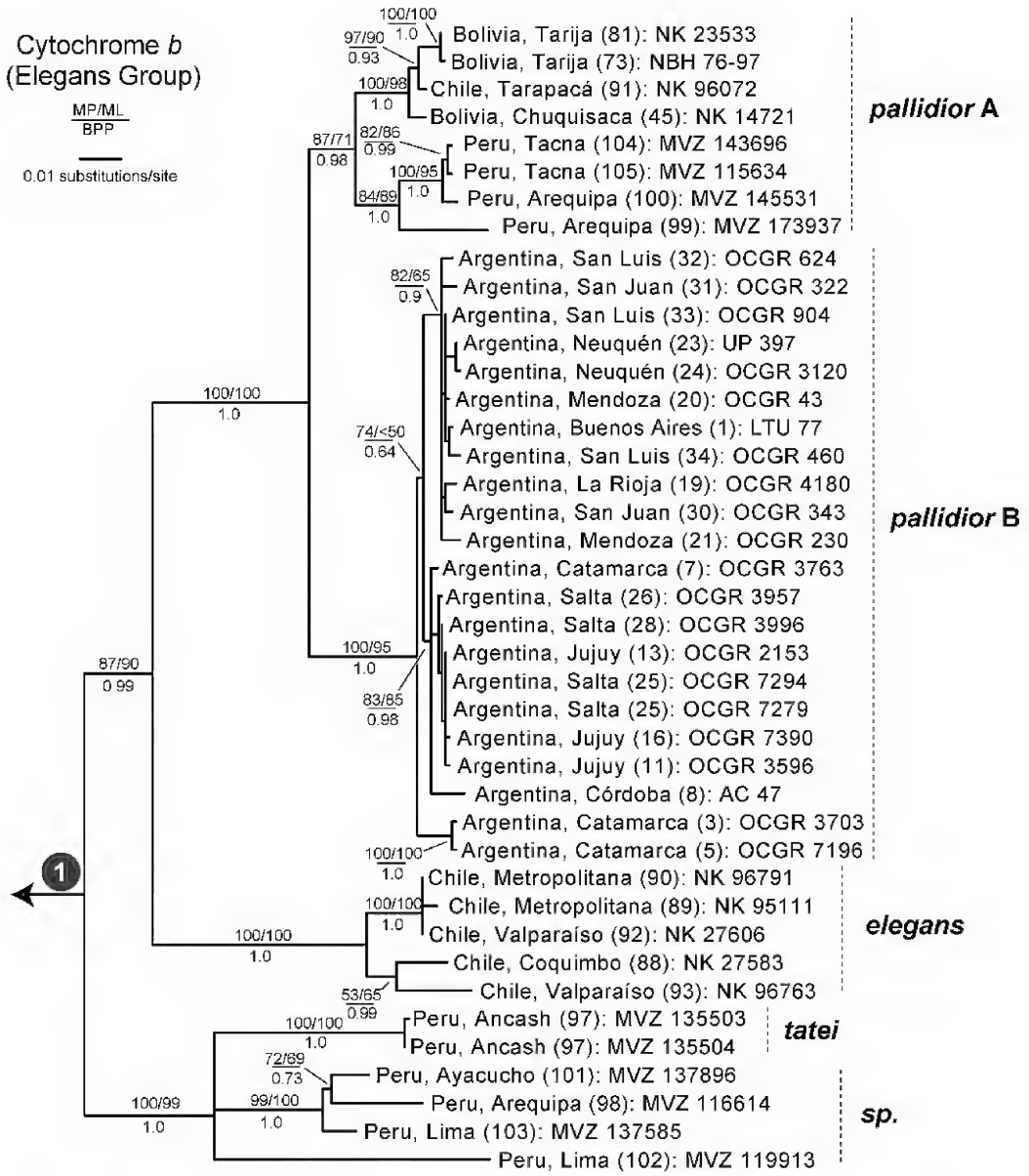
Cytochrome b
(Elegans Group)
MP/ML
BPP
0.01 substitutions/site
Bolivia, Tarija (81): NK 23533
Bolivia, Tarija (73): NBH 76-97
Chile, Tarapacá (91): NK 96072
Bolivia, Chuquisaca (45): NK 14721
Peru, Tacna (104): MVZ 143696
Peru, Tacna (105): MVZ 115634
Peru, Arequipa (100): MVZ 145531
Peru, Arequipa (99): MVZ 173937
pallidior A
Argentina, San Luis (32): OCGR 624
Argentina, San Juan (31): OCGR 322
Argentina, San Luis (33): OCGR 904
Argentina, Neuquén (23): UP 397
Argentina, Neuquén (24): OCGR 3120
Argentina, Mendoza (20): OCGR 43
Argentina, Buenos Aires (1): LTU 77
Argentina, San Luis (34): OCGR 460
Argentina, La Rioja (19): OCGR 4180
Argentina, San Juan (30): OCGR 343
Argentina, Mendoza (21): OCGR 230
Argentina, Catamarca (7): OCGR 3763
Argentina, Salta (26): OCGR 3957
Argentina, Salta (28): OCGR 3996
Argentina, Jujuy (13): OCGR 2153
Argentina, Salta (25): OCGR 7294
Argentina, Salta (25): OCGR 7279
Argentina, Jujuy (16): OCGR 7390
Argentina, Jujuy (11): OCGR 3596
Argentina, Córdoba (8): AC 47
Argentina, Catamarca (3): OCGR 3703
Argentina, Catamarca (5): OCGR 7196
pallidior B
Chile, Metropolitana (90): NK 96791
Chile, Metropolitana (89): NK 95111
Chile, Valparaíso (92): NK 27606
Chile, Coquimbo (88): NK 27583
Chile, Valparaíso (93): NK 96763
elegans
Peru, Ancash (97): MVZ 135503
Peru, Ancash (97): MVZ 135504
tatei
Peru, Ayacucho (101): MVZ 137896
Peru, Arequipa (98): MVZ 116614
Peru, Lima (103): MVZ 137585
Peru, Lima (102): MVZ 119913
sp.
1

Fig. 4. Relationships among 41 cytochrome-*b* sequences of the Elegans Group. This subtree shows the full details of relationships at node 1 (fig. 3) as resolved by ML analysis. Phylogenetic terminals in this tree are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 1). Nodal support values are provided for all nodes recovered in common by MP, ML, and BI analyses.

species, a difference of interpretation that we discuss elsewhere (see Taxonomy, below). *Thylamys pusillus* A is represented by six nonidentical sequences from the Chaco Boreal (north of the Río Pilcomayo) that exhibit an average uncorrected intraclade distance of 1.9%. Genetic variation is substantially less within *pusillus* B from the Chaco Austral (south of the Pilcomayo, 0.6%) and *pusillus* C from the Mesopotamian region of northeastern Argentina (between the Paraná and Uruguay rivers, 0.4%).

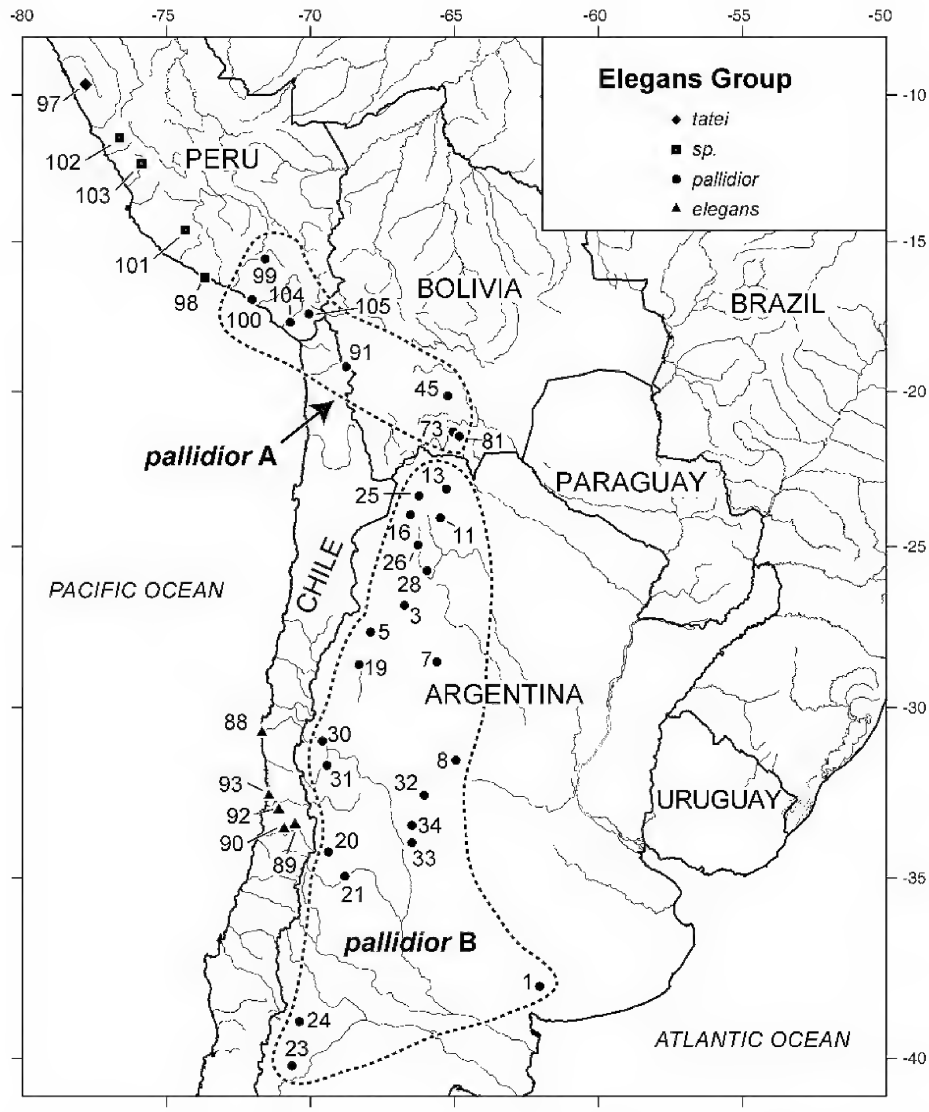

Fig. 5. Map of collecting localities for specimens of the Elegans Group sequenced for this study. Numbers are keyed to entries in the gazetteer (appendix 1).

Although the reciprocal monophyly of all three haplogroups is robustly supported by our MP and Bayesian analyses, we note that our geographic samples are tightly clustered with large unsampled gaps between them, and that the monophyly of *pusillus* A is only moderately supported by ML bootstrapping.

The Venustus Group (fig. 8) includes two species, both of which are abundantly represented in our analyses by specimens collected on the eastern Andean slopes and foothills of Bolivia and northwestern Argentina (fig. 9). Although our analyses recovered the same basal mtDNA sequence dichotomy in this group previously reported by Braun et al. (2005), we use the name *sponsorius* for the species that they called *cinderella* (see Taxonomy, below). *Thylamys sponsorius* and *T. venustus* have partially overlapping distributions, but *T. sponsorius* ranges farther south into Argentina, and *T. venustus* ranges farther north into Bolivia. Where their latitudinal ranges overlap, *T. sponsorius* tends to occur at higher elevations than *T. venustus*,

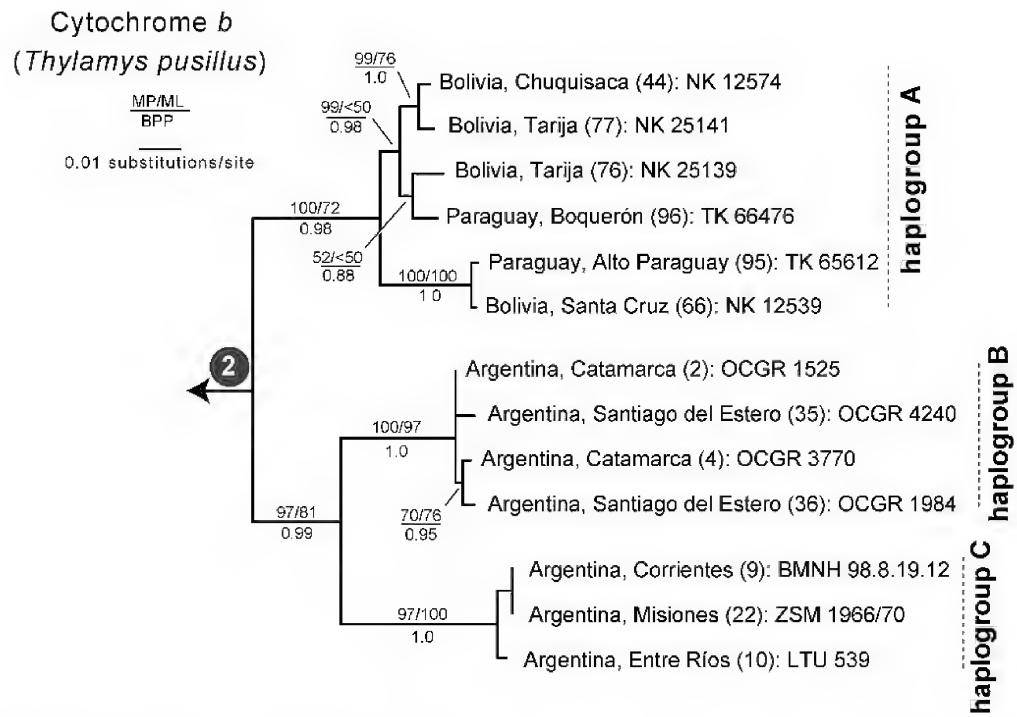

Fig. 6. Relationships among 13 cytochrome-*b* sequences of *Thylamys pusillus*. This subtree shows the full details of relationships at node 2 (fig. 3) as resolved by ML analysis. Phylogenetic terminals in this tree are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 1). Nodal support values are provided for all nodes recovered in common by MP, ML, and BI analyses.

but allopatric populations of *T. venustus* in central Bolivia can occur at elevations as high as those at which *T. sponsorius* occurs further south.

Mean intraspecific genetic diversity for *Thylamys sponsorius* is 1.8%, and specimens from Argentina form a strongly supported clade to the exclusion of conspecific Bolivian material, which appears as a shallowly branched paraphyletic group. By contrast, phylogeographic structure is much more apparent within *T. venustus*, which includes three robustly supported and spatially segregated haplogroups (fig. 10). *Thylamys venustus* A is represented by 12 sequences (with an average intraclade divergence value of 1.2%) from seven localities at high elevations (2450–4000 m) in central Bolivia, where voucher specimens were collected in the departments of La Paz, Chuquisaca, and Cochabamba. *Thylamys venustus* B is represented by 10 sequences (with an average intraclade divergence value of 1.1%) from seven localities at somewhat lower elevations (1695–2950 m) in eastern Cochabamba and western Santa Cruz. *Thylamys venustus* C is represented by 26 sequences (with an average intraclade divergence of only 0.6%) from 18 localities in foothill and middle elevations (349–2100 m) in western Santa Cruz southward to Argentina (Jujuy and Tucumán).

PHYLOGENETIC RELATIONSHIPS BASED ON CYTOCHROME *B*: In addition to resolving species-level clades and intraspecific phylogeography as described above, our analyses of cytochrome-*b* sequence data provide noteworthy support for some deeper nodes. Within the Elegans Group, for example, there is strong support for a sister-group relationship between *T. elegans* and *T. pallidior*, and for a group that includes *T. tatei* and two unnamed Peruvian lineages (fig. 4). Additionally, there is strong support for the monophyly of the genus *Thylamys*, and moderate to strong support for the monophyly of a group that includes all of

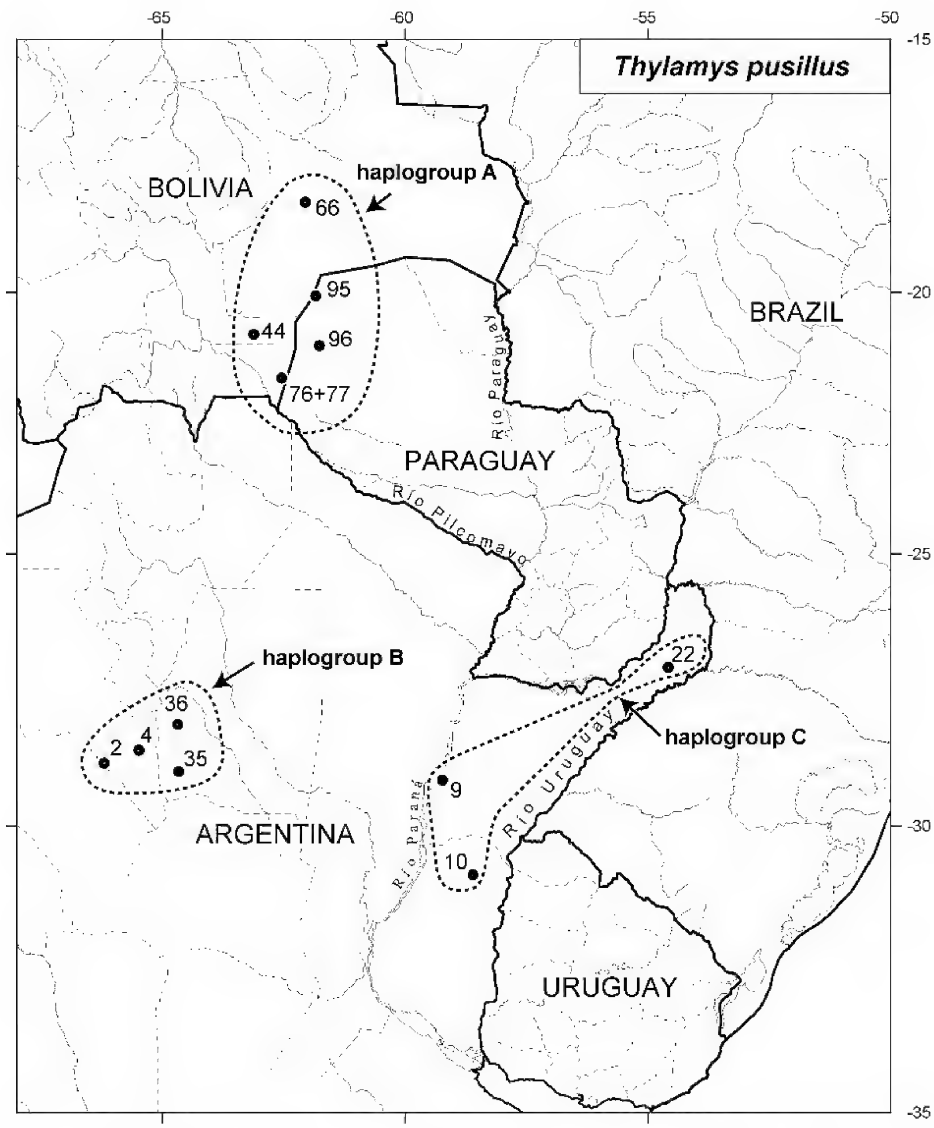

Fig. 7. Map of collecting localities for specimens of *Thylamys pusillus* sequenced for this study. Numbers are keyed to entries in the gazetteer (appendix 1).

the species of *Thylamys* except *T. velutinus* and *T. karimii* (fig. 3). However, other relationships of key interest are only moderately to weakly supported by these data. Among such equivocally resolved details are the problematic relationships of three Brazilian species (*T. velutinus, T. karimii,* and *T. macrurus*) and the sister-group relationship between the Elegans and Pusillus clusters.

PHYLOGENETIC ANALYSES OF CONCATENATED MITOCHONDRIAL SEQUENCES: Because the cytochrome-*b* dataset was unable to convincingly resolve several key interspecific relationships, we obtained ND2 and COX2 sequences from exemplars of each of the species and haplogroups described above, choosing specimens that spanned the basal split recovered for each clade in the CYTB tree. Separate analyses of the ND2 and COX2 datasets using MP, ML, and BI methods recovered topologies that were similar to those obtained from CYTB in most respects. Importantly, relationships that were strongly supported by one gene never

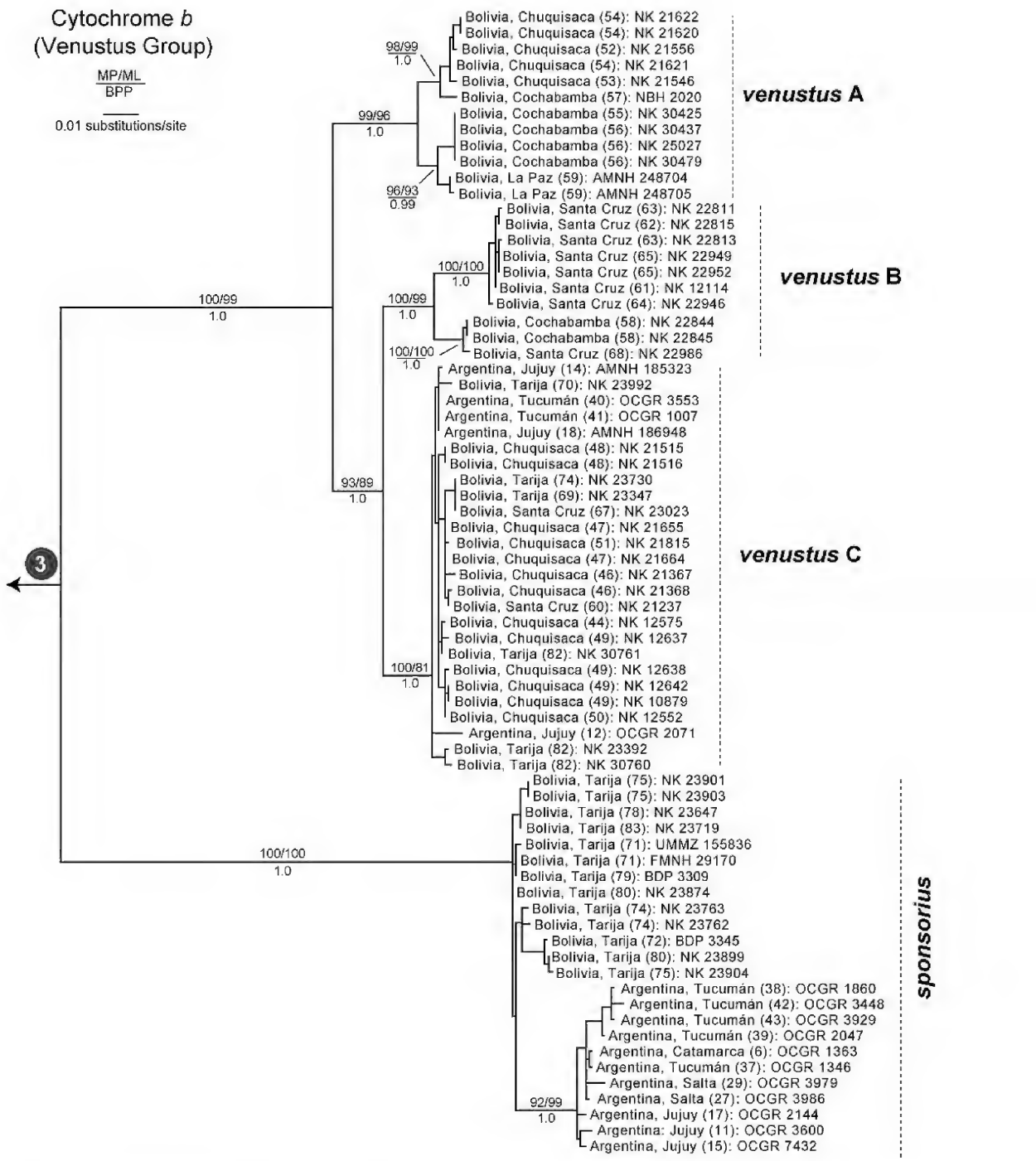

Fig. 8. Relationships among 72 cytochrome-*b* sequences of the Venustus Group. This subtree shows the full details of relationships at node 3 (fig. 3) as resolved by ML analysis. Phylogenetic terminals are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 1). Nodal support values are provided for all nodes recovered in common by MP, ML, and BI analyses.

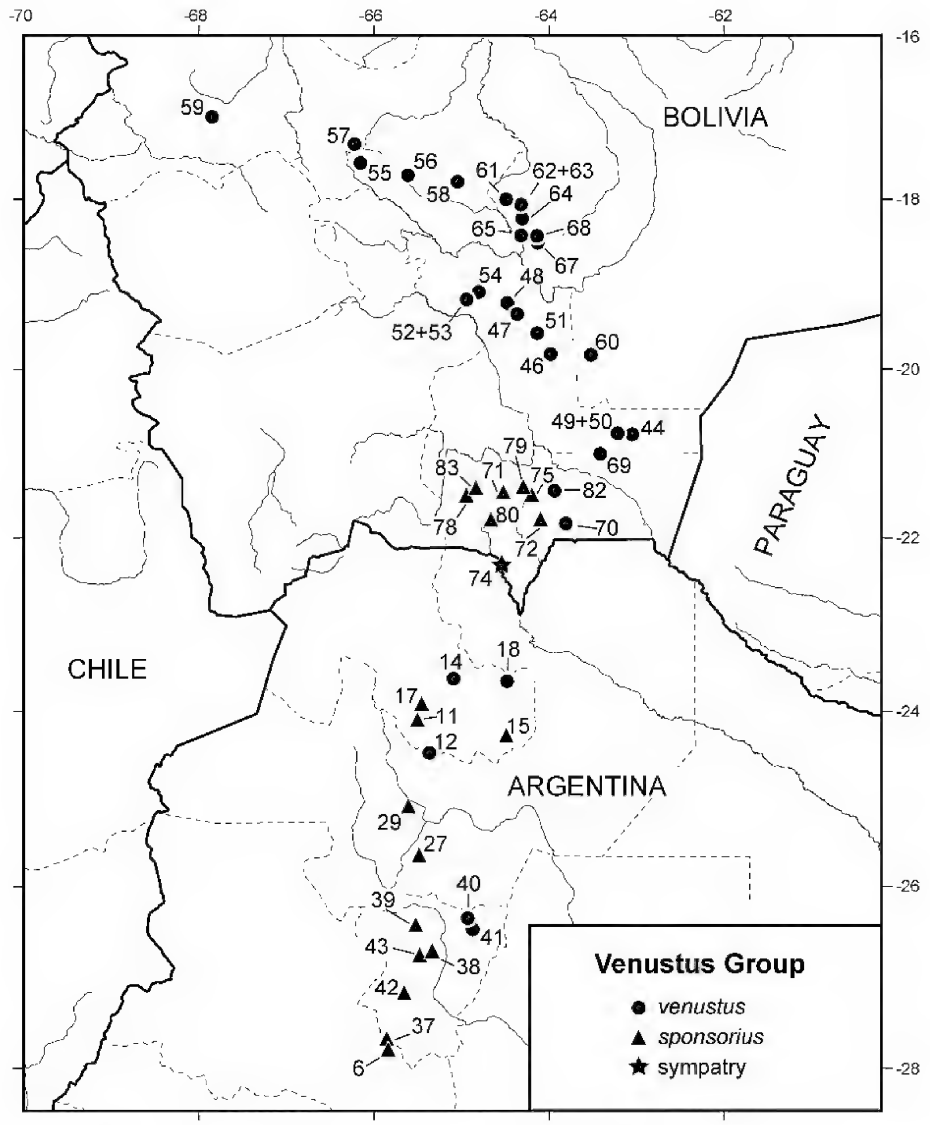

Fig. 9. Map of collecting localities for specimens of the Venustus Group sequenced for this study. Numbers are keyed to entries in the gazetteer (appendix 1).

conflicted with relationships that were strongly supported by another. This lack of hard incongruence among datasets suggests that combining these datasets is appropriate.

Maximum parsimony, maximum likelihood, and Bayesian analyses of the combined-gene (CYTB + ND2 + COX2) dataset recovered most of the same relationships obtained from cytochrome *b* and provide more robust support for clades that were only weakly or moderately supported by individual-gene analyses (fig. 11). Novel features of this topology include (1) a weakly supported basal clade that unites the Brazilian species *Thylamys velutinus* and *T. karimii*, and (2) a strongly supported sister-group relationship between *T. macrurus* and the Venustus Group (*T. sponsorius* + *T. venustus*). Additionally, most of the supraspecific nodes with moderate to strong support from CYTB (fig. 3) are consistently strongly supported by the combined-gene analyses. Among the previously described supraspecific relationships that seem conclu-

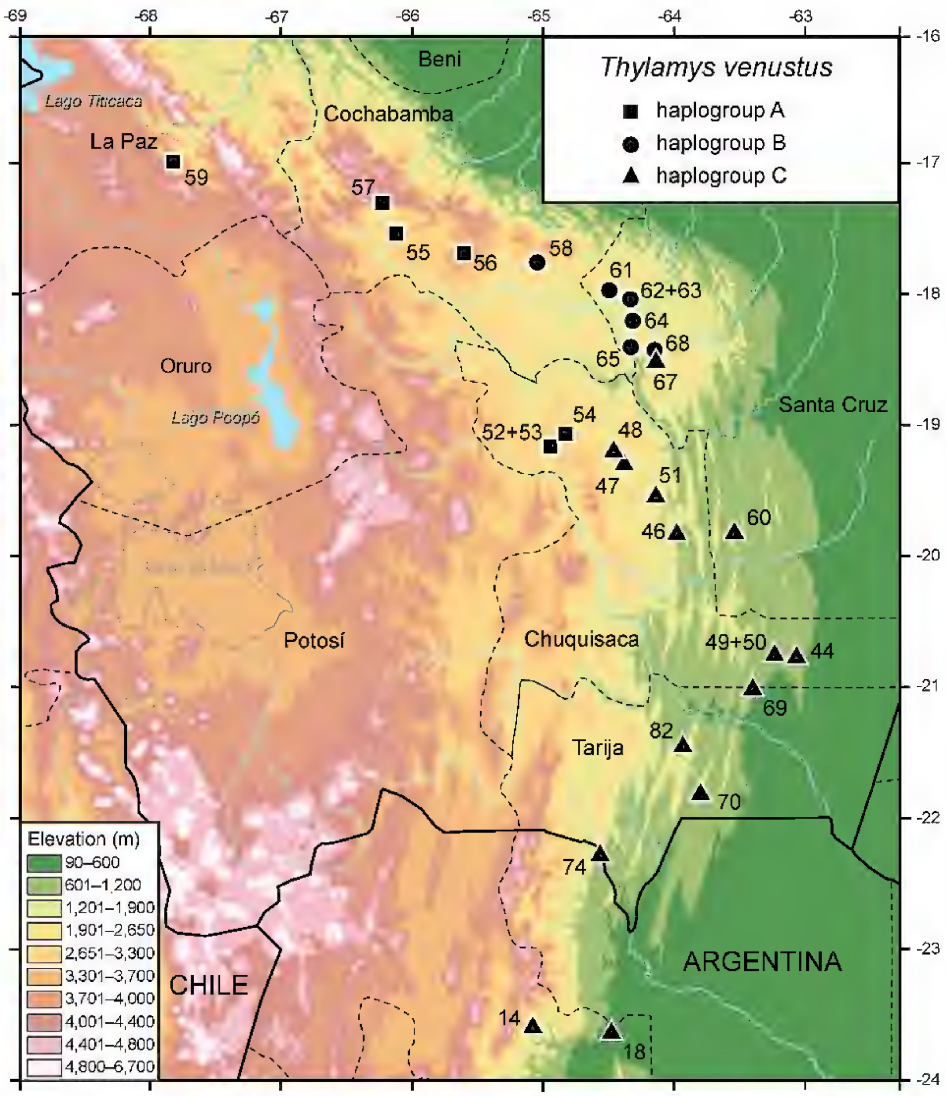

Fig. 10. Map of collecting localities for specimens from each of the three *Thylamys venustus* haplogroups from Bolivia and northern Argentina (not all Argentine collecting localities of haplogroup C are shown). Numbers are keyed to entries in the gazetteer (appendix 1).

sively resolved in these results include the monophyly of the Elegans and Venustus groups, a sister-group relationship between the Elegans Group and *Thylamys pusillus*, and a clade that includes all of the species of *Thylamys* except *T. velutinus* and *T. karimii*. Additionally, all of the species and haplogroups delineated using CYTB were recovered with very strong support in the combined-gene analyses. The single noteworthy example of a CYTB clade with diminished support in these results is *pusillus* B + *pusillus* C, which still receives strong support from MP bootstrapping, but for which ML bootstrap support and BI posterior probabilities have substantially eroded.

TOPOLOGY TESTS: Our combined-gene dataset provides a large sample of characters (2877 bp; table 4) for evaluating alternative hypotheses of phylogenetic relationships. Of these, only three are sufficiently explicit to merit statistical testing: (1) Palma et al. (2002) analyzed cytochrome-*b* sequence data from five species of *Thylamys* and recovered the

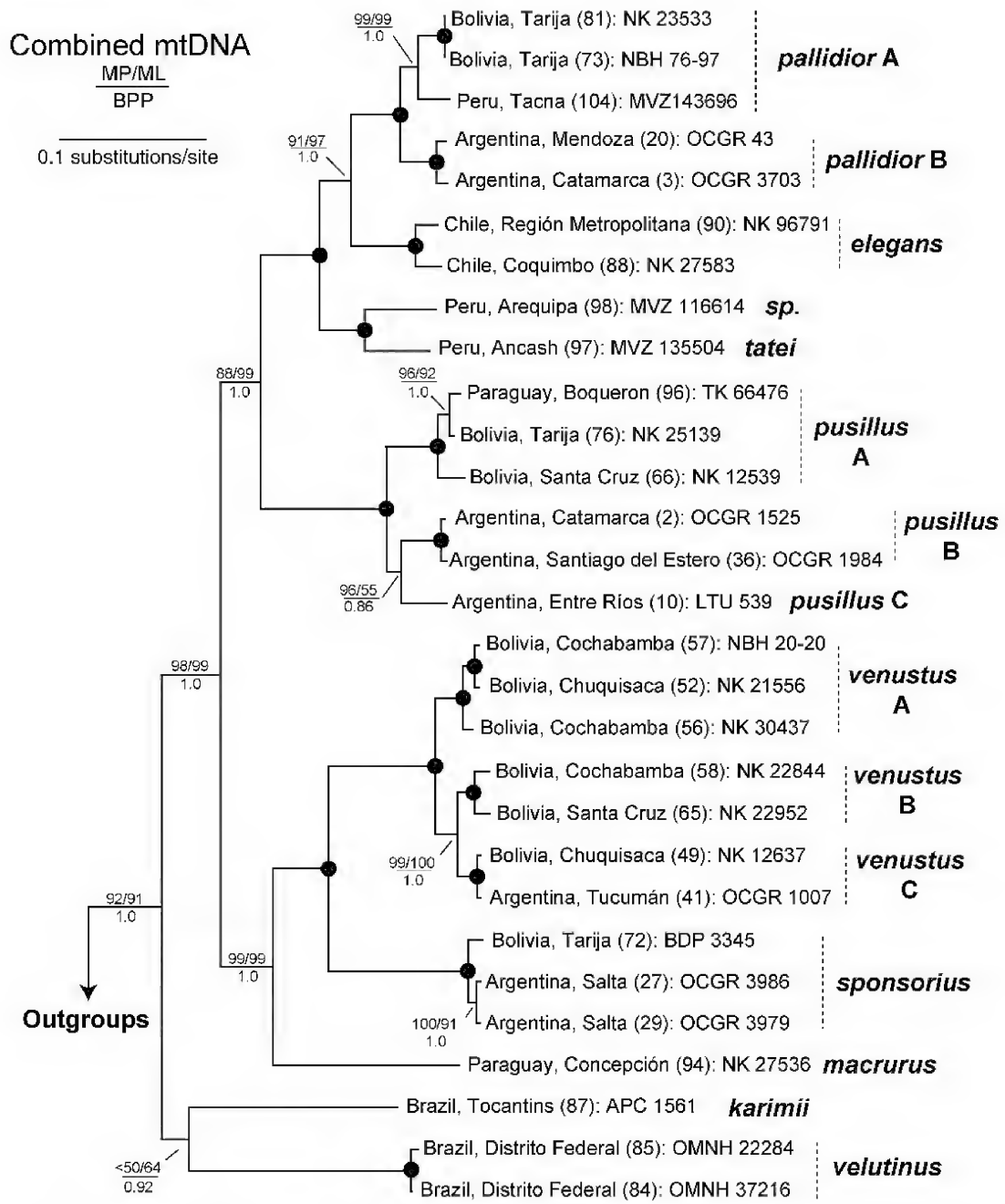

Fig. 11. The maximum likelihood tree based on concatenated sequence data from cytochrome *b*, cytochrome *c* oxidase subunit II, and NADH dehydrogenase 2 from 29 specimens representing nine species of *Thylamys* and six individuals representing five outgroup genera (GTR + I + Γ, ln-likelihood = −22234.43). Phylogenetic terminals are identified by country and state/department/province of origin, locality number (in parentheses; see appendix 1), and an alphanumeric specimen identifier (see table 1). Black circles indicate nodes with 100% ML and MP bootstrap support and Bayesian posterior probabilities equal to 1.0.

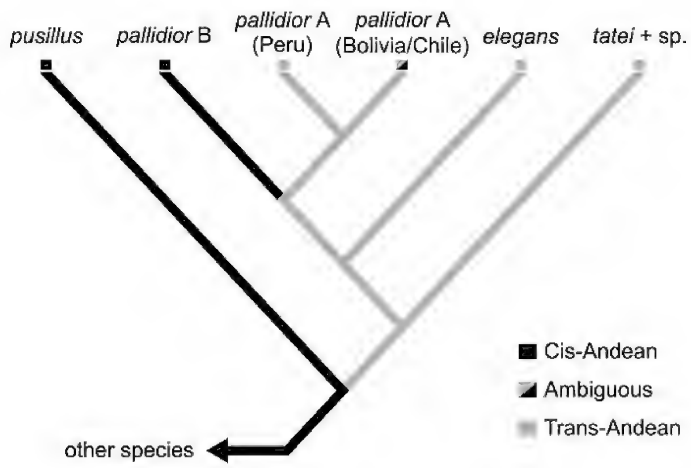

Fig. 12. Parsimony reconstruction of ancestral distributions in relation to the Andean cordillera. Branch tips are coded as east of the Andes (cis-Andean), west of the Andes (trans-Andean), or both (ambiguous). The topology used for this reconstruction is derived from fig. 11.

topology (*macrurus* (*pusillus* (*venustus* (*elegans* + *pallidior*)))), (2) Braun et al. (2005) analyzed cytochrome-*b* sequence data from seven species and recovered the topology (*macrurus* ((*venustus* + *sponsorius*) (*pusillus* (*pallidior* (*elegans* + *tatei*))))), and (3) Carvalho et al. (2009) analyzed cytochrome-*b* sequence data from eight species and recovered the topology (*macrurus* ((*sponsorius* + *venustus*) (*karimii* (*pusillus* (*pallidior* (*tatei* + *elegans*)))))). All of these hypotheses can be confidently rejected using Shimodaira and Hasegawa's (1999) likelihood-ratio test with our combined-gene data ($P = 0.00$ for all alternatives).

Although several possible explanations might account for the rejected topologies of Palma et al. (2002), Braun et al. (2005), and Carvalho et al. (2009), we noticed that the most striking discrepancies between their results and ours involve only two sequences. One sequence has GenBank accession number AF431926 and was said to have been obtained from a Paraguayan specimen of *Thylamys macrurus* (field number NK 27536). The second is AF431927, said to have been obtained from a Bolivian specimen of *T. pusillus* (NK 25139). Both sequences were originally obtained and analyzed by Palma et al. (2002), but Braun et al. (2005) and Carvalho et al. (2009) subsequently used AF431926 (downloaded from GenBank) in their analyses. Because we independently extracted and amplified cytochrome *b* from NK 27536 (*T. macrurus*) and NK 25139 (*T. pusillus*), we were able to compare our sequences with those obtained by Palma et al. (2002). Sequence alignment indicates that both of our *T. macrurus* sequences (from specimens NK 27536 and APC 932) are much more similar to each other (p-distance = 0.7%) than either is to AF431926 (average p-distance = 21.23%). A BLAST comparison of AF431926 against other sequences in GenBank reveals that its closest match to previously published data (87%) is a cytochrome-*b* sequence from *Marmosops impavidus* (U34670). A BLAST search on the purported *T. pusillus* sequence (AF431927) clearly demonstrates that it does not belong to a marsupial; instead, it is 95% identical to several GenBank sequences from the cricetid rodent *Phyllotis xanthopygus* (e.g., AY431053).

PARSIMONY ANCESTRAL-STATE RECONSTRUCTION: Ancestral areas for lineages that comprise the Elegans Group (the only clade that occurs, in part, west of the Andes) were inferred across the combined-gene ML topology using the parsimony criterion (fig. 12). Results indicate three Andean dispersal events: (1) the ancestral Elegans Group lineage dispersed from east to west and diversified along the western coast of Chile and Peru, (2) the lineage leading to *Thylamys pallidior* B later dispersed from west to east, forming a wide-ranging clade

distributed in a variety of habitats in Argentina, and (3) a subclade of *T. pallidior* A invaded the altiplano of Bolivia and Chile (along the crest of the Andes, and therefore of ambiguous classification with respect to our cis/trans dichotomy).

MORPHOLOGICAL CHARACTER VARIATION

Among the 287 morphological specimens (tissue vouchers, types, and other unsequenced material) examined in the course of this project, we discovered taxonomic variation in qualitative characters of the integument, skull, and dentition. We describe and illustrate this variation in the accounts that follow. The material on which our morphological observations are based is listed in the taxonomic accounts of the next section.

External Characters

DORSAL PELAGE PATTERN: Most marsupials have two distinct body pelage color zones, dorsal and ventral, with a more or less abrupt line of transition between them. In this "bicolored" phenotype, the middorsal fur may be indistinctly darker than the lateral fur, but the transition is gradual, not abrupt. By contrast, *Lestodelphys* and most species of *Thylamys* are "tricolored" (sensu Tate, 1933: 209) because a distinctly darker middorsal color zone is separated from a distinctly paler lateral color zone along a line of demarcation that extends on each side from a point on the forehead posteriorly to the rump. Most specimens with tricolored pelage also have a dark axillary spot behind the foreleg on each side.

Among the specimens of *Thylamys* that we examined, the tricolor pattern was consistently absent only in *T. velutinus*, which is uniformly brownish dorsally without any sharp pigmental difference between the middorsal and lateral fur. Our observations in this respect are consistent with those of Tate (1933: 234) and Carmignotto and Monfort (2006), who likewise noted the taxonomically unusual pelage pigmentation of this species. Although Carmignotto and Monfort (2006) suggested that the tricolor pattern is indistinct in another species, *T. karimii,* the specimens of *T. karimii* that we examined had unmistakably tricolored fur.

VENTRAL PELAGE PATTERN: The ventral pelage of many small didelphids consists of hairs that are either "self-colored"—having the same pale (whitish or yellowish) coloration from base to tip—or they are gray based. Gray-based hairs are, as the term implies, grayish basally, but they are abruptly paler (usually whitish or yellowish) distally. In some species of *Thylamys* (e.g., *T. pusillus*) the entire ventrum is covered with self-colored hairs, but in others (e.g., *T. elegans*) a median streak of self-colored ventral fur is bordered by broad lateral zones of gray-based fur; in three species (*T. sponsorius, T. velutinus,* and *T. venustus*) almost all of the ventral fur is gray based.

MANUAL CLAWS: The claws of the manus are short, not extending beyond the fleshy apical pad of each digit in some species of *Thylamys*, but in other species the claws are much longer and extend well beyond the fleshy fingertips. Short-clawed species include *T. macrurus* (fig. 13B), *T. pusillus*, and members of the Venustus Group (*T. sponsorius, T. venustus*). Long-clawed species include *T. karimii*, *T. velutinus* (fig. 13A), and members of the Elegans Group (*T. elegans*, *T. pallidior*, *T. tatei*). Confident scoring of manual claw length is best accomplished under low magnification to ensure that claws are undamaged (neither broken nor blunted) and that fleshy fingertips (on dried skins) are not unduly distorted.

MANUAL PLANTAR PADS: Six fleshy pads (thenar, hypothenar, and four interdigital pads; Brown and Yalden, 1973) are present on the ventral (plantar) surface of the manus in most didelphids. In most species of *Thylamys* (e.g., *T. macrurus*; fig. 13B) these six pads are separated from one another by deep folds of elastic skin, and they surround a concave central palmar surface; the apex of each pad is covered by specialized (nontubercular) epidermis bearing dermatoglyphs (friction or papillary ridges) like those on human fingertips. *Thylamys karimii* and *T. velutinus* (fig. 13A), however, differ from other congeners in having the interdigital and carpal pads fused together, in lacking a concave central palmar surface, and in the marked reduction (*T. velutinus*) or

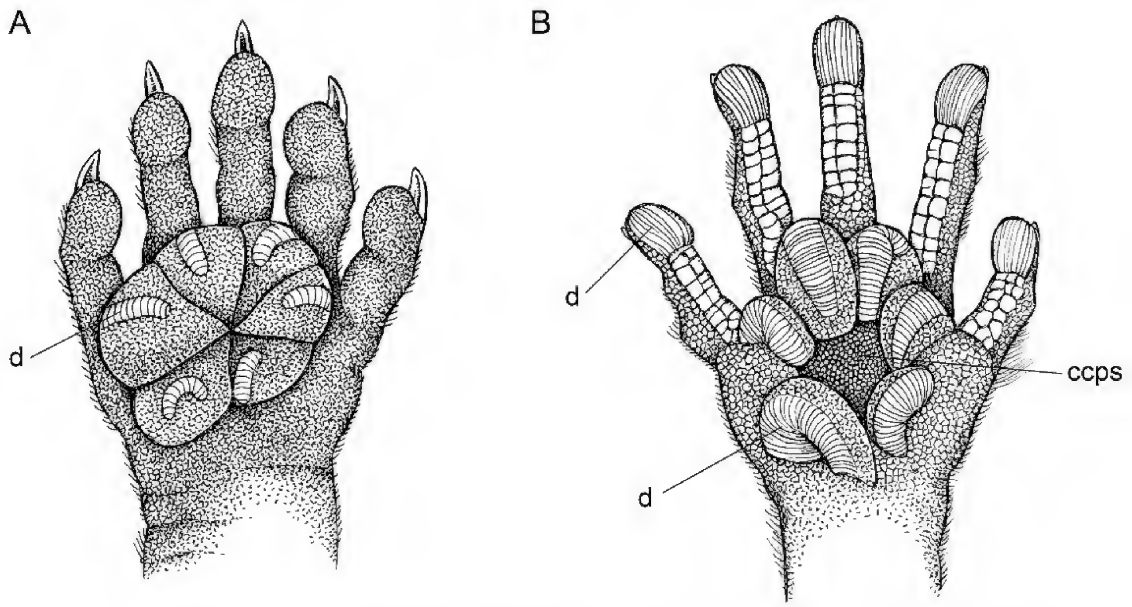

Fig. 13. Ventral views of right manus illustrating taxonomic differences in plantar morphology and claw length (see text). In *Thylamys velutinus* (**A,** based on ZMUC 166 and 167), almost the entire plantar surface is tubercular, with vestigial dermatoglyphs (**d**) restricted to the apices of the plantar pads; the latter are fused together and extend inward to the center of the palm, which lacks a concave central area. The claws are long in this species, extending well beyond the fleshy finger tips. In *T. macrurus* (**B,** MZUSP 32097) dermatoglyphs are more extensive on the fingertips and on the plantar pads, the plantar pads are separate and surround a concave central palmar surface (**ccps**), and the claws are short, not extending much beyond the fleshy tip of each digit.

absence (*T. karimii*) of plantar dermatoglyphs.

PALE TAIL TIP: All species of *Thylamys* have a bicolored tail that is dark (brownish or grayish) above and abruptly paler (whitish) on the ventral surface. In most species, the dark dorsal coloration extends all the way to the tip of the tail, but the tail tip is pale (whitish) above and below for several millimeters in most examined specimens of *T. macrurus* and *T. tatei*, and in some specimens of *T. pusillus* from northeastern Argentina.

CAUDAL PREHENSILE SURFACE: In most species of *Thylamys*, the ventral surface of the tail is provided with a hairless prehensile surface consisting of a shallow median groove and an apical pad bearing dermatoglyphs (Carmignotto and Monfort, 2006: fig. 4c). However, in *T. karimii* (op. cit.: fig. 4a) and *T. velutinus* (op. cit.: fig. 4b) the median groove is indistinct or absent and the apical pad, although hairless, lacks dermatoglyphs.

Craniodental Characters

NASAL LENGTH: Although we measured nasal length as a quantitative variable, measurement values do not capture all of the information suggested by visual inspection of skulls, so we also coded how far the nasal bones extend posteriorly with respect to a line drawn across the caudal limits of the right and left lacrimals (fig. 14). Nasals were scored as *short* if these bones did not extend posteriorly as far as the lacrimals, *long* if they terminated at about the same level as the lacrimals, and *very long* if they terminated well behind the lacrimals.

Intraspecific variation in this character was often noted, but some taxonomic variation in trait frequencies are noteworthy (table 7). Whereas most species of *Thylamys* have long or very long nasals, *T. elegans* usually has short nasals, as do most examined specimens of *T. velutinus*. Interestingly, *T. pallidior* lacks an obviously modal condition for this char-

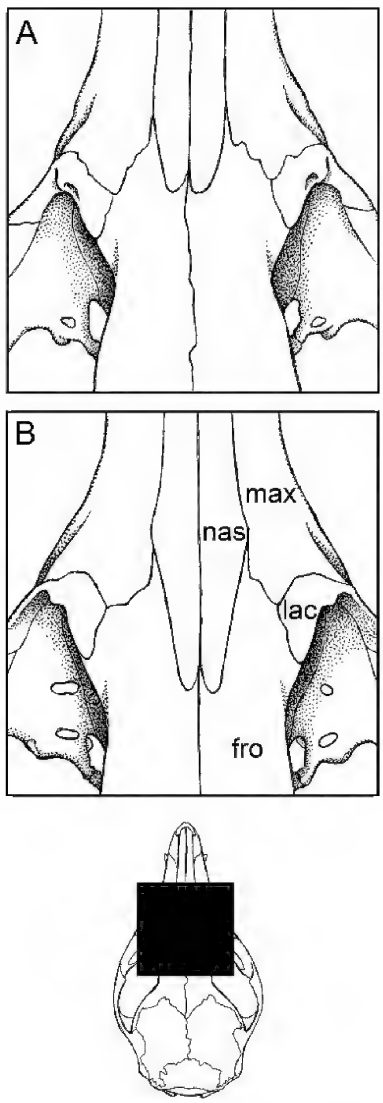

Fig. 14. Dorsal view of interorbital region illustrating taxonomic differences in the posterior extension of the nasal bones (**nas**) with respect to the lacrimals (**lac**). In *Thylamys elegans* (**A,** UWBM 44446) the nasals are short, not extending as far posteriorly as the lacrimals, whereas the lacrimals of *T. tatei* (**B,** MVZ 135506) are longer, extending posteriorly behind the lacrimals. Other abbreviations: **fro,** frontal; **max,** maxillary.

acter: all three nasal morphologies were observed in roughly equal numbers of specimens, even within haplotypes from restricted parts of the species' geographic range (i.e., the tabulated variability is not the result of pooling geographically variable samples).

TABLE 7
Variation in Nasal Morphology among Species of *Thylamys*[a]

	N[b]	Short	Long	Very long
elegans	24	21 (88%)	3 (12%)	
karimii	6		1 (17%)	5 (83%)
macrurus	4		2 (50%)	2 (50%)
pallidior	47	15 (32%)	18 (38%)	14 (30%)
pusillus	35		11 (31%)	24 (69%)
sponsorius[c]	14	2 (14%)	5 (36%)	7 (50%)
tatei	11		3 (27%)	8 (73%)
velutinus	6	4 (67%)	2 (33%)	
venustus[c]	25	2 (8%)	8 (32%)	15 (60%)

[a]See text for trait definitions.
[b]Number of adult specimens scored for this character.
[c]Only tissue vouchers scored.

LACRIMAL FORAMINA: All examined specimens of *Thylamys* have two lacrimal foramina on each side, but there is taxonomic variation in the position of these paired openings. In some species the lacrimal foramina are more or less concealed from lateral view because they open inside the anterior orbital margin (fig. 15B), but in others the foramina are laterally exposed because they are outside the orbit (fig. 15A). We also recognize an intermediate condition in which the anteroventral foramen is exposed and the posterodorsal foramen is concealed (fig. 15C). Most species exhibit variation in this character, but there are potentially useful taxonomic differences (table 8). For example, the lacrimal foramina are consistently concealed in *T. tatei*, but one or both foramina are exposed in most examined specimens of *T. elegans*, and both foramina are prominently exposed in most specimens of *T. velutinus*.

INFRAORBITAL FORAMEN: In most didelphids, and in many species of *Thylamys*, the infraorbital foramen opens above P3 (fig. 15B) or above the commissure between P3 and M1 (fig. 15A). One or both of these taxonomically widespread traits were observed in all examined specimens of *T. karimii, T. macrurus, T. pusillus, T. tatei,* and *T. velutinus* (table 9). By contrast, the infraorbital foramen opens above M1 in most examined specimens of *T. elegans* and *T. pallidior* (fig. 15C), and this trait was also observed in a few specimens of the Venustus Group (*T. sponsorius* and *T. venustus*).

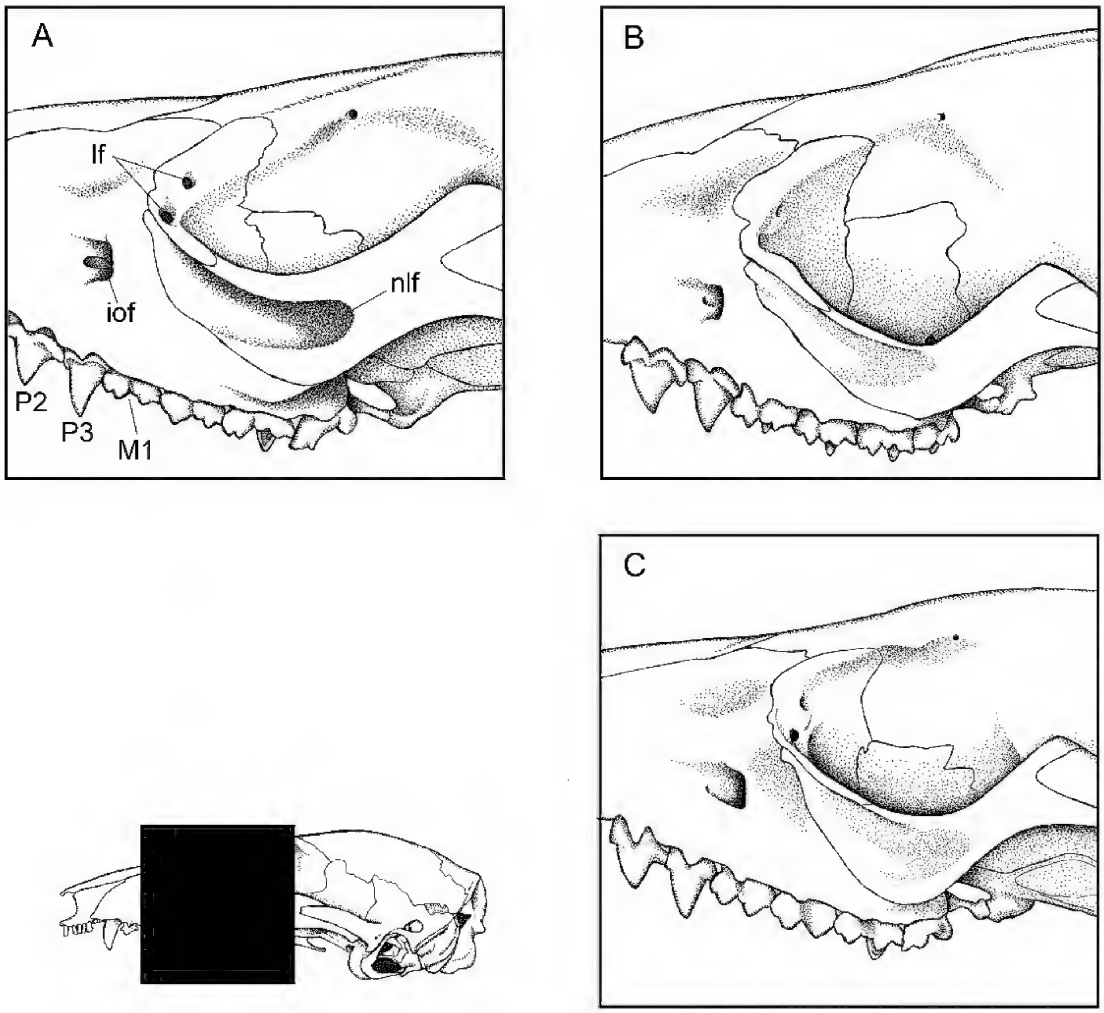

Fig. 15. Left lateral cranial views illustrating taxonomic differences in the position of the infraorbital foramen (**iof**) above the tooth row, in the position of the lacrimal foramina (**lf**) with respect to the orbit, and in depth of the nasolabial fossa (**nlf**). In *Thylamys velutinus* (**A,** OMNH 22284) the infraorbital foramen is usually above P3 or above the P3/M1 commissure, the lacrimal foramina are laterally exposed anterior to the orbit, and the nasolabial fossa is deeply excavated. In *T. pusillus* (**B,** AMNH 260025) the infraorbital foramen is usually above P3, the lacrimal foramina are often concealed inside the orbit, and the nasolabial fossa is shallow. In *Thylamys pallidior* (**C,** AMNH 262406) the infraorbital foramen is usually above M1, the lacrimal foramina are often partially exposed, and the nasolabial fossa is shallow.

NASOLABIAL FOSSA: The concave lateral surface of the jugal just below the orbit is the site of origin for M. maxillonasolabialis (also known as M. zygomaticus; Coues, 1872). The nasolabial fossa[2] is shallow, inconspicuous, and lacks sharply defined borders in most species of *Thylamys*—for example, in *T. pusillus* (fig. 15B) and *T. pallidior* (fig. 15C). By contrast, the fossa is deeply excavated (with sharply defined dorsal, ventral, and caudal margins) and dorsoventrally narrower in *T. velutinus* (fig. 15A).

SUPRAORBITAL MARGINS: The dorsolateral contours of the frontal bones between the orbitotemporal fossae are smoothly rounded or squared in most species of *Thylamys*, but

[2] Minkoff et al. (1979: 54) referred to this concavity as the "maxillary fossa," but because it primarily occupies the jugal, we prefer to call it the nasolabial fossa (after Filan, 1990).

TABLE 8
Exposure of the Lacrimal Foramina among Species of *Thylamys*[a]

	N[b]	Exposed	Intermediate	Concealed
elegans	24	8 (33%)	15 (63%)	1 (4%)
karimii	6		4 (67%)	2 (33%)
macrurus	4		3 (75%)	1 (25%)
pallidior	47	6 (13%)	27 (57%)	14 (30%)
pusillus	35	1 (3%)	12 (34%)	22 (63%)
sponsorius[c]	14		4 (29%)	10 (71%)
tatei	11			11 (100%)
velutinus	6	4 (67%)	2 (33%)	
venustus[c]	25	4 (16%)	10 (40%)	11 (44%)

[a]See text for trait definitions.
[b]Number of adult specimens scored for this character.
[c]Only tissue vouchers scored.

some species have supraorbital "beads" (upturned lateral margins flanked by shallow grooves; see Voss and Jansa, 2009: fig. 11B). We observed supraorbital beads on all examined adult specimens of *T. karimii* and most examined adult specimens of *T. macrurus* and *T. pusillus*, but beading occurs infrequently in other species (table 10). Beading is clearly subject to ontogenetic variation because juveniles and subadults seldom have beads, even in species that usually have them as adults, and they tend to be better developed among old adult specimens than among conspecific young adults. In some large adult male specimens of *T. karimii, T. macrurus,* and *T. pusillus,* supraorbital beads

TABLE 9
Variation in the Position of the Infraorbital Foramen among Species of *Thylamys*[a]

	N[b]	Above P3	Above P3/M1	Above M1
elegans	24		4 (17%)	20 (83%)
karimii	6	6 (100%)		
macrurus	4	1 (25%)	3 (75%)	
pallidior	47		11 (23%)	36 (77%)
pusillus	35	31 (89%)	4 (11%)	
sponsorius[c]	14	4 (29%)	7 (50%)	3 (21%)
tatei	11	6 (55%)	5 (45%)	
velutinus	6	3 (50%)	3 (50%)	
venustus[c]	25	15 (60%)	8 (32%)	2 (8%)

[a]See text for trait definitions.
[b]Number of adult specimens scored for this character.
[c]Only tissue vouchers scored.

TABLE 10
Variation in Interorbital Morphology among Species of *Thylamys*[a]

	N[b]	Rounded/ squared	Beaded
elegans	24	23 (96%)	1 (4%)
karimii	6		6 (100%)
macrurus	4	1 (25%)	3 (75%)
pallidior	47	42 (89%)	5 (11%)
pusillus	35	11 (31%)	24 (69%)
sponsorius[c]	14	14 (100%)	
tatei	11	10 (91%)	1 (9%)
velutinus	6	6 (100%)	
venustus[c]	25	23 (92%)	2 (8%)

[a]See text for trait definitions.
[b]Number of adult specimens scored for this character.
[c]Only tissue vouchers scored.

project laterally to form small postorbital processes.

We did not tabulate "rounded" and "squared" as alternative states because we often observed intermediate conditions that were hard to classify. Most young animals (e.g., juveniles, subadults, young adults) have rounded supraorbital margins, whereas squared supraorbital margins normally occur in older animals. Such age-correlated conspecific differences were sometimes interpreted taxonomically by Tate (1933) who, for example, characterized "*Marmosa janetta*" (all examined specimens of which were old adults) as having sharp supraorbital margins.

MAXILLARY FENESTRAE: Most didelphids have several sets of bilaterally paired palatal perforations, some of which (foramina) transmit nerves, blood vessels, or other soft-tissue structures, whereas others (fenestrae) do not transmit anything. Incisive foramina, maxillopalatine fenestrae, palatine fenestrae, and posterolateral palatal foramina (fig. 16) are invariably present in *Thylamys*. By contrast, maxillary fenestrae—perforations in the maxillary bone lateral to the maxillopalatine openings—are normally present in some species but not in others.

Maxillary fenestrae are consistently present in examined specimens of *Thylamys karimii, T. macrurus, T. sponsorius,* and *T. velutinus*, but they are usually also present in *T. pusillus* and *T. venustus* (table 11). By contrast, maxillary fenestrae are consistently

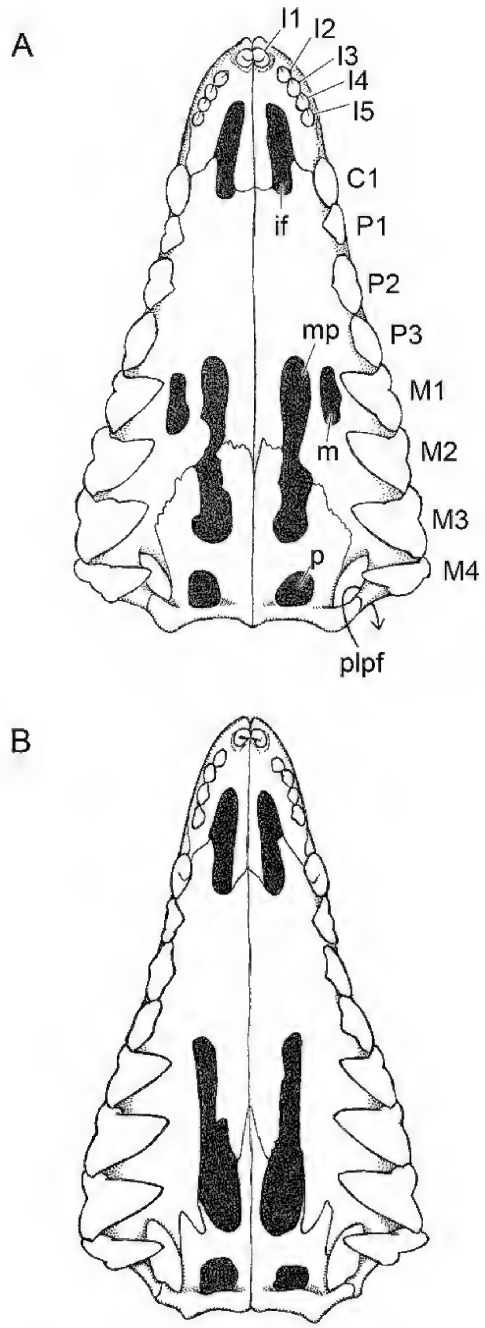

Fig. 16. Palatal morphology of *Thylamys venustus* (**A,** AMNH 261254) and *T. pallidior* (**B,** UMMZ 155831). Maxillary fenestrae (**m**) are usually present in *T. venustus*, but they are almost always absent in *T. pallidior*. Other abbreviations: **if**, incisive foramen; **mp**, maxillopalatine fenestra; **p**, palatine fenestra; **plpf**, posterolateral palatal foramen.

TABLE 11
Variation in the Occurrence of Maxillary Fenestrae among Species of *Thylamys*[a]

	N[b]	Bilaterally present	Unilaterally present	Absent
elegans	24			24 (100%)
karimii	6	6 (100%)		
macrurus	8	8 (100%)		
pallidior	47	2 (4%)	2 (4%)	43 (91%)
pusillus	58	50 (86%)	2 (3%)	6 (10%)
sponsorius[c]	13	13 (100%)		
tatei	11	1 (9%)		10 (91%)
velutinus	6	6 (100%)		
venustus[c]	24	23 (96%)	1 (4%)	

[a]See text for trait definitions.
[b]Number of adult specimens scored for this character.
[c]Only tissue vouchers scored.

absent in examined specimens of *T. elegans*, and they are usually absent in *T. pallidior* and *T. tatei*. In most examined specimens of all species, maxillary fenestrae are either bilaterally present or bilaterally absent; unilateral presence of maxillary fenestrae is rare.

UPPER SECOND INCISOR: In most species of *Thylamys* the crowns of I2–I5 increase in size from front to back, a progression that is most easily seen in lateral view. In specimens conforming to this morphology, the crown of I2 is visibly smaller than or subequal to the crown of I3 (fig. 17B). However, in all examined specimens of *T. tatei* with unworn or lightly worn teeth, I2 is visibly larger that I3 (fig. 17A), an apparently unique trait of this species.

STYLAR CUSP C: The stylar shelf of didelphid upper molars is provided with a series of five or six small cusps along the labial margin. By convention, these cusps are given alphabetic designations based on positional criteria (Clemens, 1966). The most consistently recognizable are stylar cusp B (labial to the paracone) and stylar cusp D (labial to the metacone). One or two small cusps that are posterolabial to the paracone and anterolabial to the metacone correspond to stylar cusp(s) C. In some species of *Thylamys*, there is no distinct cusp in the C position, and in these taxa the ectoflexus (a labial indentation in the stylar shelf) is deeper and more distinct than it is in taxa with stylar cusp C. The presence of stylar cusp C

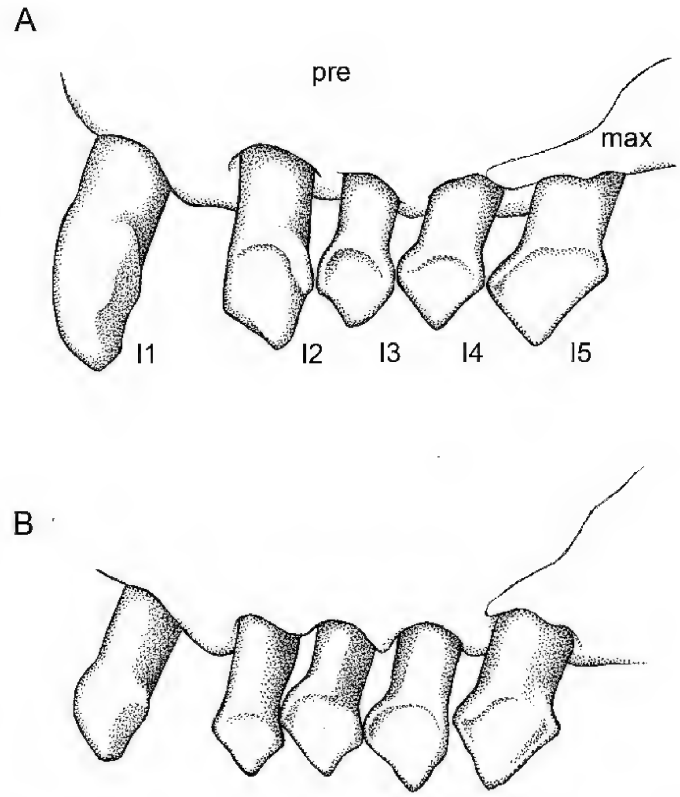

Fig. 17. Labial view of left upper incisor row of *Thylamys tatei* (**A,** MVZ 135507), with I2 larger than I3; and *T. elegans* (**B,** AMNH 97755), with I2 smaller than I3. Abbreviations: **pre,** premaxillary; **max,** maxillary.

contributes to the "serrated" appearance of the stylar shelf as noted by authors (Solari, 2003; Carmignoto and Monfort, 2006). Because stylar cusp C may be present or absent at different dental loci, we scored this character separately on M1 and M2 (table 12); due to frequent polymorphism and lack of useful taxonomic differences, we did not score this trait on M3. Minimally worn (juvenile, subadult, or young adult) teeth are necessary for confident scoring of this character.

METACONULE: The metaconule, a small but taxonomically important occlusal element of the primitive tribosphenic molar bauplan (Simpson, 1936), is absent or indistinct in most didelphids (Voss and Jansa, 2009), as it is in most species of *Thylamys*. In species conforming with this widespread opossum phenotype (including *T. elegans, T. karimii, T. pallidior, T. sponsorius, T. tatei,* and *T. venustus*; table 13), the metaconule appears (if at all) only as a small chevron on the postprotocrista that is just barely visible when the newly erupted or lightly worn teeth of juveniles and subadults are viewed under high magnification; presumably because such diminutive structures are quickly obliterated by wear, adult teeth seldom retain any clearly identifiable vestige of the metaconule. By contrast, the metaconule is often substantially larger and ontogenetically persistent in *T. pusillus* and *T. velutinus*, and a well-developed metaconule was likewise observed in the single specimen of *T. macrurus* that we were able to score for this character.

TAXONOMY

Twenty-one nominal species-group taxa are based on Recent material of *Thylamys* (table 14). Among these we recognize nine

TABLE 12
Variation in the Occurrence of Stylar Cusp C on M1 and M2 among Species of *Thylamys*[a]

		M1			M2		
	N[b]	+/+	+/−	−/−	+/+	+/−	−/−
elegans	23	1 (4%)		22 (96%)	1 (4%)		22 (96%)
karimii	12	5 (42%)	5 (42%)	2 (16%)	7 (58%)	2 (17%)	3 (25%)
macrurus	6	5 (83%)	1 (17%)		6 (100%)		
pallidior	43		1 (2%)	42 (98%)	1 (2%)	2 (5%)	40 (93%)
pusillus	41	32 (78%)	5 (12%)	4 (10%)	36 (88%)	3 (7%)	2 (5%)
sponsorius[c]	15	1 (7%)		14 (93%)			15 (100%)
tatei	11	2 (18%)	4 (36%)	5 (45%)		4 (36%)	7 (64%)
velutinus	5	5 (100%)			5 (100%)		
venustus[c]	31	5 (16%)	4 (13%)	22 (71%)	13 (42%)	2 (6%)	16 (52%)

[a]Trait abbreviations: +/+, present on right and left teeth; +/−, present on right or left tooth, absent on other; −/−, absent on right and left teeth.

[b]Number of specimens scored for this character (including juveniles, but excluding old adults with worn occlusal features).

[c]Only tissue vouchers scored.

valid species in two subgenera based on the molecular analyses and correlated patterns of morphological character variation reported above. The following accounts summarize what is known about geographic distributions, provide morphological diagnoses and comparisons, discuss relevant nomenclatural issues, and suggest where additional research is needed to explore apparent discrepancies between molecular and morphological patterns of character variation.

Except as noted otherwise above (see Morphological Character Variation), all of the species that we refer to *Thylamys* conform to the morphological description of the genus provided by Voss and Jansa (2009: 138–140). Therefore, our taxonomic diagnoses are restricted to characters that serve to distinguish congeneric species as recognized herein. Because most cited characters exhibit intraspecific polymorphism (see tables 7–13), effective identification is necessarily based on combinations of traits. Problems that might be encountered in attempting to distinguish closely related forms are discussed at length under the Comparisons heading in each account.

TABLE 13
Variation in the Occurrence of Metaconules among Species of *Thylamys*[a]

	N[b]	Absent	Small	Well-developed
elegans	23	23 (100%)		
karimii	3	3 (100%)		
macrurus	1			1 (100%)
pallidior	30	27 (90%)	3 (10%)	
pusillus	36		6 (17%)	30 (83%)
sponsorius[c]	12	12 (100%)		
tatei	8	8 (100%)		
velutinus	5		2 (40%)	3 (60%)
venustus[c]	27	23 (85%)	4 (15%)	

[a]See text for trait definitions.

[b]Number of specimens scored for this character.

[c]Only tissue vouchers scored.

All of the species now referred to *Thylamys* were originally described as members of the genus *Didelphis* (sometimes misspelled "*Didelphys*" in the older literature) or *Marmosa*. The history of their subsequent binomial combinations is recorded in synonymies provided by Creighton and Gardner (2008), so this information is not repeated below. Instead, our remarks on nomenclature are primarily concerned with species-level issues, including past misidentifications that are inconsistent with current understanding of geographic distributions.

***Xerodelphys*, new subgenus**

TYPE SPECIES: *Thylamys karimii*.

CONTENTS: *Thylamys karimii* and *T. velutinus*.

TABLE 14
Nominal Species-group Taxa Referred to *Thylamys*, Type Specimens, and Type Localities[a]

	Type specimen	Type locality
bruchi Thomas, 1921	BMNH 21.4.21.8[b]	Argentina: San Luis, Alto Pencoso
cinderella Thomas, 1902	BMNH 0.7.9.20[b]	Argentina: "Tucuman"
citellus Thomas, 1912	BMNH 98.8.19.9[b]	Argentina: Corrientes, Goya
coquimbensis Tate, 1931	FMNH 23302[b]	Chile: Coquimbo, Paiguano
elegans Waterhouse, 1839	BMNH 53.8.29.18[c]	Chile: "Valparaiso"
fenestrae Marelli, 1932	MACN 14955[d]	Argentina: Buenos Aires, Tornquist, Abra de la Ventana
griseus Desmarest, 1827	UMMZ 125243[e]	Paraguay: Amambay, 28 km SW Pedro Juan Caballero
janetta Thomas, 1926	BMNH 26.1.1.167[b]	Bolivia: Tarija, Carlazo
karimii Petter, 1968	MNHN 1968-148[b]	Brazil: Pernambuco, Exu
macrurus Olfers, 1818	UMMZ 125243[e]	Paraguay: Amambay, 28 km SW Pedro Juan Caballero
nanus Olfers, 1818	MVZ 144311[e]	Paraguay: Boquerón, 460 km NW Villa Hayes
pallidior Thomas, 1902	BMNH 2.2.2.116[b]	Bolivia: Oruro, Challapata
pimelura Reinhardt, 1851	ZMUC 164[f]	Brazil: Minas Gerais, Lagoa Santa
pulchellus Cabrera, 1934	MLP 21-X-35-32[b]	Argentina: Santiago del Estero, Robles
pusillus Desmarest, 1804	MVZ 144311[e]	Paraguay: Boquerón, 460 km NW Villa Hayes
soricinus Philippi, 1894	unknown[g]	Chile: "Valdivia"
sponsorius Thomas, 1921	BMNH 21.1.1.85[b]	Argentina: Jujuy, Sunchal
tatei Handley, 1957	USNM 302915[b]	Peru: Ancash, Chasquitambo
velutinus Wagner, 1842	NMW B-2621[h]	Brazil: São Paulo, Ipanema ("Ypanema")
venustus Thomas, 1902	BMNH 2.1.1.120[b]	Bolivia: Cochabamba, Parotani ("Paratani")
verax Thomas, 1921	BMNH 20.12.18.34[b]	Paraguay: Presidente Hayes, Misión Central[i]

[a]Only available names are listed. Names of species recognized as valid in this report are in boldface. The gender of epithets originally published in combination with feminine generic names (*Didelphis* and *Marmosa*) has been changed to agree with *Thylamys* (masculine). Full bibliographic information for all names is provided in Gardner (2008).

[b]Holotype by original designation.

[c]The specimen currently recognized as the type (e.g., by Tate, 1933; Jenkins and Knutson, 1983) is one of several—all collected by Darwin at Valdivia—that Waterhouse (1839) may have examined. Of these putative syntypes, Thomas (1888: 354) selected one (specimen "e" in his list) as the "type" (lectotype according to the Code; ICZN, 1999: Article 4). Handwritten annotations in Thomas's personal copy of his catalog identify specimen "e" as BMNH 53.8.29.18 (P. Jenkins, personal commun.).

[d]Neotype (Martin, 2009).

[e]Neotype (Voss et al., 2009).

[f]Lectotype (Tate, 1933: 234).

[g]Based on a mounted specimen formerly preserved in the Museo Nacional de Historia Natural in Santiago, Chile (Osgood, 1943). Possibly still extant, but catalog number and preservation unknown.

[h]Holotype by monotypy (Pelzeln, 1883: 115).

[i]Verbatim type locality is "Mision, west of Concepcion" in the "Northern Chaco of Paraguay" (Thomas, 1921: 521).

DIAGNOSIS: Members of the subgenus *Xerodelphys* can be distinguished from other congeners (herein referred to the nominotypical subgenus, see below) by their reduction or loss of plantar dermatoglyphs, lack of a concave central palmar surface, tails that are shorter than the combined length of head and body, and absence of distinct modifications for caudal prehension (table 15).

REMARKS: Although the monophyly of *Xerodelphys* is only weakly supported by phylogenetic analyses of our concatenated-

TABLE 15
Morphological Comparisons among *Thylamys (Xerodelphys) karimii*, *T. (X.) velutinus*, and Members of the Subgenus *Thylamys*

	karimii	*velutinus*	Subgenus *Thylamys*[a]
Body pelage	tricolored	bicolored	tricolored
Ventral fur	self-white	gray-based	variable[b]
Manual claws	long	long	variable[b]
Manual dermatoglyphs	absent	vestigial	well-developed
Central palmar surface	absent	absent	present
Tail	< HBL	< HBL	≥ HBL
Caudal prehensile surface	vestigial	vestigial	well-developed
Nasolabial fossa	shallow	deeply excavated	shallow

[a]Including *Thylamys macrurus, T. pusillus,* and members of the Elegans and Venustus groups.
[b]Varies taxonomically (see table 16).

gene dataset (fig. 11), the absence of a concave central palmar surface (resulting from fusion of plantar pads on the manus) and the reduction or loss of plantar dermatoglyphs are unique in the family Didelphidae and provide supporting evidence that these two species form a clade. Sequence data from nuclear loci will presumably allow future tests of this hypothesis.

The morphological distinctness of the taxa we refer to *Xerodelphys* was previously recognized by Solari (2003), who, however, regarded *karimii* as a synonym of *velutinus*. Carmignotto and Monfort (2006) were the first to clearly identify the diagnostic traits that distinguish *T. karimii* and *T. velutinus* from each other and from congeneric species that we refer to the nominotypical subgenus, but they prudently refrained from naming a new genus-group taxon in the absence of a supporting phylogenetic analysis. We commend their restraint and credit them with the morphological observations on which our subgeneric diagnosis is based.

Thylamys karimii (Petter, 1968)

SYNONYMS: None.

DISTRIBUTION: According to Carmignotto and Monfort (2006), who examined much more material than we have seen, *Thylamys karimii* inhabits open (nonforest) Cerrado and Caatinga landscapes in the Brazilian states of Bahia, Goiás, Mato Grosso, Minas Gerais, Pernambuco, Piauí, Rondônia, and Tocantins; it has also been collected in the Distrito Federal. Although no Bolivian specimens are known, *T. karimii* could be expected to occur on the Serranía de Huanchaca in Santa Cruz department, where other Cerrado endemics have recently been discovered (Emmons et al., 2006). The geographic range of *T. karimii* overlaps that of *T. velutinus* (see Carmignotto and Monfort, 2006: fig. 7), but these species have yet to be collected sympatrically.

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present) in all specimens examined by us, but perhaps less distinctly so in other material (Carmignotto and Monfort, 2006); ventral pelage entirely self-white, usually without lateral zones of gray-based hairs; plantar pads of manus fused together (concave central palmar surface absent) and uniformly covered with small tubercles (plantar dermatoglyphs absent); manual claws long, extending well beyond fleshy apical pads of digits; tail much shorter than combined length of head and body (LT/HBL × 100 = 77%; N = 32 [based on measurement data from Carmignotto and Monfort, 2006: table 1]), without pale tip; ventral prehensile surface of tail tip absent. Nasals usually very long (extending posteriorly beyond lacrimals); lacrimal foramina partially exposed to lateral view on orbital margin in most specimens; infraorbital foramen above P3; nasolabial fossa usually shallow (deeply excavated in a few specimens); supraorbital margins beaded; maxillary fenestrae present; crown of second upper

incisor (I2) smaller than or subequal to crown of I3; stylar cusp C often present on M1 and M2; metaconule indistinct or absent on M3.

COMPARISONS: *Thylamys karimii* can be distinguished unambiguously from *T. velutinus*, the only other member of the subgenus *Xerodelphys*, by its self-white ventral pelage (the ventral pelage is entirely gray based in *velutinus*), and complete lack of plantar dermatoglyphs (vestigial dermatoglyphs are present at the apex of each plantar pad in *velutinus*). Cranial character differences are difficult to evaluate with the small samples at hand, but the nasal bones appear to be absolutely longer on average (NL = 11.6–13.4 mm; $N = 5$) in *karimii* than in *velutinus* (LN = 11.3–11.7 mm; $N = 3$) and they usually project posteriorly well behind the lacrimals (the nasals do not extend posteriorly beyond the lacrimals in any examined specimen of *velutinus*; table 7). Although we observed supraorbital beads in *karimii* that we did not see in *velutinus*, Carmignotto and Monfort (2006) reported beaded interorbitals in specimens of *velutinus* that we have not examined. Whereas metaconules were indistinct or absent in all three specimens of *karimii* that we were able to score confidently for this character, distinct metaconules were present in all five scored specimens of *velutinus* (table 13).

Comparisons of measurement data between larger samples of *Thylamys karimii* and *T. velutinus* than we were able to examine are provided in Carmignotto and Monfort's (2006) exemplary study. Briefly, *T. karimii* is larger than *T. velutinus* in most measured dimensions, but it has absolutely and relatively smaller canines, a difference that is conspicuous in side-by-side comparisons. Despite broad overlap in most univariate morphometric comparisons, *T. karimii* and *T. velutinus* can be separated into nonoverlapping clusters by canonical discriminant functions analysis (Carmignotto and Monfort, 2006: fig. 8).

REMARKS: Originally described as a valid species by Petter (1968), *karimii* was subsequently listed as a synonym of *Thylamys pusillus* by Gardner (1993), whereas Palma (1995) and Solari (2003) treated it as a synonym of *T. velutinus*. Carmignotto and Monfort (2006) effectively refuted these synonymies by identifying most of the characters that we now recognize as distinguishing *karimii* from other species of *Thylamys* (table 15).

Three specimens of small didelphids collected near Exu in the Brazilian state of Ceará were misidentified as *Marmosa karimii* by Mares et al. (1981) and Streilein (1982). The single specimen from this series that we examined (CM 80015, from 0.5 km S Exu) is an old adult male *Gracilinanus agilis*, whereas two others examined by A.P. Carmignotto (in litt., 8 March 2010) are *Cryptonanus agricolai*: one is MZUSP 16610 (an immature female from Fazenda Guaraní, 2.9 km N Exu), and the other is MZUSP 16961 (an adult male from Escola Agricola, 0.7 km S Exu). Behavioral observations based on these specimens were erroneously attributed to *Thylamys karimii* by Creighton and Gardner (2008) despite Palma's (1995) well-founded doubts about their correct identification.

SPECIMENS EXAMINED ($N = 12$): **Brazil**—*Mato Grosso,* Chapada dos Guimarães (ANSP 4632), 264 km N Xavantina (BMNH 76.632–76.639; USNM 393536–393538).

Thylamys velutinus (Wagner, 1842)

SYNONYMS: *pimelurus* Reinhardt, 1851.

DISTRIBUTION: According to Carmignotto and Monfort (2006), *Thylamys velutinus*, which is only known from a few localities, occurs in Cerrado habitats in the Brazilian states of Goiás, Minas Gerais, and São Paulo; it has also been collected in the Distrito Federal. This species is not known to occur sympatrically with any other congener, although it could be expected to coexist with *T. karimii* throughout much of its geographic range.

MORPHOLOGICAL DIAGNOSIS: Body pelage bicolored (abrupt line of transition from darker middorsal to paler lateral coloration absent); ventral pelage completely gray based (superficially buffy or whitish) except on chin; plantar pads of manus fused together (concave central palmar surface absent) and almost completely covered with small tubercles (small plantar dermatoglyphs are present at the apex of each pad); manual claws long, extending well beyond fleshy apical pads of

digits; tail much shorter than combined length of head and body (LT/HBL × 100 = 79%; $N = 6$ [based on measurement data from Carmignotto and Monfort, 2006: table 1]), without pale tip; ventral prehensile surface of tail tip indistinct or absent. Nasal bones usually short, not extending posteriorly behind lacrimals in any examined specimen; lacrimal foramina usually exposed to lateral view anterior to orbit; infraorbital foramen above P3 or above P3/M1 commissure; nasolabial fossa deeply excavated; supraorbital margins rounded or squared, not beaded in any examined specimen; maxillary fenestrae present; crown of second upper incisor (I2) subequal to crown of I3; stylar cusp C consistently present on M1 and M2; metaconule present on M3.

COMPARISONS: Qualitative and morphometric comparisons with *Thylamys karimii*, the only other member of the subgenus *Xerodelphys*, were provided by Carmignotto and Monfort (2006). The most consistently useful of these are summarized in the preceding species account.

REMARKS: Although *velutinus* has always been recognized as a valid species, other forms have been regarded as junior synonyms by authors. Of these, only *pimelurus* is clearly conspecific (Tate, 1933; Carmignotto and Monfort, 2006). By contrast, *formosa* Shamel, 1930, listed as a subspecies of *velutinus* by Cabrera (1958), is a morphologically distinctive taxon of still-uncertain phylogenetic relationships; it is currently referred to the monotypic genus *Chacodelphys* (see Voss et al., 2004; Voss and Jansa, 2009).

SPECIMENS EXAMINED ($N = 7$): **Brazil**—*Distrito Federal,* Brasilia (OMNH 37216), 25 km S Brasilia (OMNH 22284); *Minas Gerais,* Lagoa Santa (UZM 164 [holotype of *pimelurus*], 165–168).

Subgenus *Thylamys* Gray, 1843

TYPE SPECIES: *Thylamys elegans* (Waterhouse, 1839).

CONTENTS: Seven species, as recognized below.

REMARKS: Monophyly of the subgenus *Thylamys* is strongly supported by phylogenetic analyses of mtDNA sequence data (fig. 11). Although none of the morphological traits that distinguish this subgenus from *Xerodelphys* (table 15) optimize as synapomorphies on the best current estimate of thylamyine relationships (Voss and Jansa, 2009: fig. 36), resolution of the still-uncertain relationships of *Chacodelphys* could change this situation. Because *Chacodelphys, Lestodelphys,* and *Xerodelphys* are all short-tailed taxa that lack a distinct caudal prehensile surface, phylogenies that include the nested clades (*Chacodelphys* (*Lestodelphys* (*Xerodelphys* (*Thylamys*)))) could constrain character optimizations such that a relatively long tail (≥ HBL) and well-developed caudal prehensile surface would be synapomorphic for the subgenus *Thylamys*.

Thylamys macrurus (Olfers, 1818)

SYNONYMS: *griseus* Desmarest, 1827; *marmotus* Oken, 1816 (unavailable).

DISTRIBUTION: *Thylamys macrurus* is only known from eastern Paraguay and the adjacent Brazilian state of Mato Grosso do Sul. Published range maps based on correctly identified material of this species are in Carmignotto and Monfort (2006: fig. 7), Creighton and Gardner (2008: map 50), and Voss et al. (2009: fig. 3). Additional Brazilian records that we assume to be valid were reported by Cáceres et al. (2007). As noted by Voss et al. (2009), a Bolivian record (in Anderson, 1997) and a record from NE Argentina (mapped by Brown, 2004) are based on misidentifications. Voss et al. (2009: 417–418) discussed the problematic ecological interpretation of capture records for this species, which has been taken in arborescent Cerrado habitats in Brazil but in second-growth moist forest in Paraguay. This species is not known to occur sympatrically with any other congener.

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage self-white (or -whitish), usually with narrow lateral zones of gray-based fur; plantar pads of manus separate, surrounding concave central palmar surface, and with well-developed dermatoglyphs; manual claws short, not extending much if at all beyond fleshy apical pads of digits; tail much longer than combined length

TABLE 16
Morphological Comparisons among Species and Species Groups of *Thylamys* (subgenus *Thylamys*)[a]

	macrurus	*pusillus*	Elegans Group[b]	Venustus Group[c]
Ventral fur	gray-based + self-white	self-white	variable[d]	gray-based[e]
Manual claws	short	short	long	short
Maxillary fenestrae	present	present	absent	present
Stylar cusp C	present	present	absent	absent/indistinct
Metaconules	well-developed	well-developed	absent/indistinct	absent/indistinct
Molar length (LM)	6.1–6.6 mm	4.8–5.8 mm	5.3–6.4 mm	5.6–6.4 mm

[a]Only modal states are tabulated (most characters exhibit some polymorphism).
[b]Including *T. elegans*, *T. pallidior*, and *T. tatei*.
[c]Including *T. sponsorius* and *T. venustus*.
[d]Varies taxonomically (see table 18).
[e]Except in "*janetta*" (see text).

of head and body (LT/HBL × 100 = 123%; $N = 5$), with pale tip (terminal 10–50 mm whitish above and below); ventral prehensile surface of tail tip well developed. Nasal bones long (extending posteriorly as far as lacrimals) or very long (extending posteriorly beyond lacrimals); lacrimal foramina partially exposed on orbital margin or concealed inside orbit; infraorbital foramen above P3 or above P3/M1 commissure; nasolabial fossa shallow; supraorbital margins usually beaded, the beads sometimes developed as postorbital processes in old adult males; maxillary fenestrae present; crown of second upper incisor (I2) smaller than or subequal to crown of I3; stylar cusp C almost always present on M1 and M2; metaconule distinct on M3 (but only one specimen confidently scored for this trait).

COMPARISONS: *Thylamys macrurus* has been described as the largest species in the genus (Solari, 2003; Carmignotto and Monfort, 2006), but it exhibits broad morphometric overlap with some species in the Elegans and Venustus groups, from which it is more readily distinguished by qualitative external and craniodental characters (table 16). Within the nominotypical subgenus, *macrurus* is qualitatively similar to *pusillus* (both species usually have beaded supraorbital margins, maxillary fenestrae, stylar cusp C on M1 and M2, and a distinct metaconule on M3), but *macrurus* is much larger (e.g., with nonoverlapping molar measurements; table 16), usually has narrow lateral zones of gray-based ventral fur (the ventral pelage is entirely self-white in *pusillus*), a pale tail tip (usually absent in *pusillus*), and shorter posterolateral palatal foramina (see Carmignotto and Monfort, 2006: fig. 6).

REMARKS: The complex nomenclatural history of this species was reviewed by Voss et al. (2009), who designated a neotype and tabulated measurement data from most of the known adult and subadult specimens. A detailed morphological description based on freshly collected Brazilian material was provided by Carmignotto and Monfort (2006), who also tabulated measurement data and illustrated craniodental traits not depicted in this report.

SPECIMENS EXAMINED ($N = 11$): **Brazil**—*Mato Grosso do Sul*, Campo Grande (MZUSP 3782), Fazenda Califórnia (MZUSP 32094, 32095, 32096), Fazenda Santa Terezinha (MZUSP 32097). **Paraguay**—*Amambay*, 28 km SW Pedro Juan Caballero (UMMZ 125243 [neotype], 125259, 125260); *Central*, Asunción (BMNH 99.11.17.1); *Concepción*, 7 km NE Concepción (MSB 70700); *Paraguarí*, Sapucay (BMNH 3.4.7.21).

Thylamys pusillus (Desmarest, 1804)

SYNONYMS: *bruchi* Thomas, 1921; *citellus* Thomas, 1912; *nanus* Oken, 1816 (unavailable); *nanus* Olfers, 1818; *pulchellus* Cabrera, 1934; *verax* Thomas, 1921.

DISTRIBUTION: This lowland species (all examined specimens are from <1000 m above sea level) occurs in southeastern

Bolivia, western Paraguay, and northern Argentina. Based on material that we examined, the distribution of *Thylamys pusillus* is almost coextensive with the tropical and subtropical dry forests and savannas collectively known as the Chaco, but a few collection localities (in the Argentine provinces of Mendoza, Misiones, and San Luis) are just outside the limits of the Chaco as that biome is conventionally recognized by authors (e.g., Short, 1975). Records of this species from Patagonian habitats (Birney et al., 1996) are based on misidentifications, as are Anderson's (1997) records from high elevations in the Bolivian department of Chuquisaca (see Remarks, below) and, apparently, a single published record from Uruguay (González et al., 2000; see Teta et al., 2009). Brown's (2004: fig. 88) map of the range of *T. pusillus* includes numerous extralimital records, all of which are apparently based on misidentifications or erroneous synonymies.[3]

The known geographic range of *Thylamys pusillus* overlaps that of *T. pallidior* in northern Argentina, where the two species have been collected sympatrically in the Reserva Biósfera de Ñacuñán (ca. 34°S, 68°W) in Mendoza province. The range of *T. pusillus* also overlaps that of *T. venustus* in southeastern Bolivia, where these species have been collected sympatrically near Carandaytí (gazetteer locality 44) in Chuquisaca department, and near Villa Montes (21°15′S, 63°30′W) in Tarija department.

[3] Brown's (2004) erroneous records for *Thylamys pusillus* include (1) Anderson's (1997) misidentified specimens of *T. venustus* (see Remarks, below) from high elevations in Chuquisaca department, Bolivia; (2) Thomas's (1912) and Tate's (1933) use of *"Marmosa marmota"* (erroneously listed as a synonym of *T. pusillus*) for specimens of *T. macrurus* collected in eastern Paraguay; (3) Brazilian specimens of *T. karimii* (erroneously synonymized with *T. pusillus* by Gardner, 1993); (4) Birney et al.'s (1996) misidentified Patagonian specimens of *T. pallidior* (see Remarks, below); (5) Cope's (1889) report of "*Philander pusillus*" (based on ANSP 4632 [*Thylamys karimii*]) from Chapada dos Guimarães in the Brazilian state of Mato Grosso; and (6) Mares et al.'s (1981) report of "*Marmosa karimii*" (based on MZUSP 16961 [*Cryptonanus agricolai*]; see Remarks, below) from Pernambuco. The basis for Bertoni's (1914, 1939) cited reports of "*Marmosa pusilla*" from Puerto Bertoni in Alto Paraná, Paraguay is unknown, but Bertoni may have used *pusilla* in the sense of Thomas (1888, 1900), who applied this epithet to specimens that are now placed in *Cryptonanus* and *Gracilinanus* (see Voss et al., 2009).

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage entirely self-white (yellowish in some museum specimens); plantar pads of manus separate, surrounding concave central palmar surface, and with well-developed dermatoglyphs; manual claws short, not extending much if at all beyond fleshy apical pads of digits; tail longer than combined length of head and body (LT/HBL $\times$ 100 = 116%; N = 30), without pale tip; ventral prehensile surface of tail tip well developed. Nasal bones long (extending posteriorly as far as lacrimals) or very long (extending beyond lacrimals); lacrimal foramina usually concealed inside orbit or partially exposed on orbital rim; infraorbital foramen usually above P3; nasolabial fossa shallow; supraorbital margins often beaded, the beads sometimes laterally expanded as postorbital processes in old male specimens; maxillary fenestrae usually present; crown of second upper incisor (I2) consistently smaller than or subequal to crown of I3; stylar cusp C usually present on M1 and M2; metaconule usually well developed on M3.

COMPARISONS: *Thylamys pusillus* can be distinguished from other members of the nominotypical subgenus by a unique combination of qualitative external and craniodental characters (table 16). Additionally, *pusillus* is smaller than most other species in the subgenus *Thylamys* (LM = 4.8–5.8 mm; N = 58), and the skull is unusually wide relative to its length, a distinctive proportion that is conspicuous in side-by-side cranial comparisons (Voss et al., 2009: fig. 5).

Thylamys pusillus has previously been confused with two other small congeners with self-white ventral pelage, *T. karimii* and *T. pallidior*. Diagnostic morphological differences between *T. pusillus* and *T. karimii,* first clearly stated by Carmignotto and Monfort (2006), are effectively summarized in our diagnosis of the subgenus *Xerodelphys* (above) and need not be repeated here. By contrast, morphological comparisons between *T. pusillus* and *T. pallidior,* although discussed in substantive detail by Voss et al. (2009), merit additional comment based on the larger samples of both species examined for this study.

Thylamys pusillus and *T. pallidior* are most reliably distinguished externally by claw length: whereas the manual claws of *pusillus* are short, not extending much (if at all) beyond the fleshy apical pads of the digits, those of *pallidior* are substantially longer, projecting well beyond the fleshy fingertips. Additionally, *pusillus* is, on average, shorter furred than *pallidior.* Among 53 measured adult specimens of *pusillus*, the middorsal fur ranges in length from 6–11 mm, but most specimens (79%) have middorsal fur that is only 7–9 mm long. By contrast, among 44 measured adult specimens of *pallidior,* the middorsal fur ranges in length from 10–15 mm, but most specimens (82%) have fur that is 11–13 mm long. Although a couple of millimeters' difference in average fur length does not sound like much, the contrast is visibly and tactilely apparent with representative specimens of both species in hand. A third external difference that might be useful for field identification concerns ventral pelage color, which is completely self-white in almost all examined specimens of *pusillus*, whereas narrow lateral zones of gray-based hairs are often present in *pallidior*.

Tables 7–13 document modal differences between *Thylamys pusillus* and *T. pallidior* in several craniodental characters, notably including infraorbital foramen position (usually over P3 in *pusillus*, usually over M1 in *pallidior*), maxillary fenestrae (usually present in *pusillus*, usually absent in *pallidior*), stylar cusp C (usually present in *pusillus,* usually absent in *pallidior*), and metaconules (usually well developed in *pusillus*, usually indistinct or absent in *pallidior*). These species are additionally distinguished by cranial proportions described and illustrated by Voss et al. (2009: 421, fig. 5).

Although no single qualitative craniodental character unambiguously distinguishes *Thylamys pusillus* from *T. pallidior* (contra Voss et al. [2009], who examined smaller series of both species), specimens that are atypical in one character are seldom atypical in others. For example, USNM 390033, a Paraguayan specimen that we identify as *pusillus* despite its lack of maxillary fenestrae, exhibits most of the other distinctive characteristics of the species, including completely self-white ventral pelage, short claws, weakly beaded supraorbital margins, infraorbital foramen above P3, well developed stylar cusp C on M1 and M2, and a well-developed metaconule on M3. Thus, specimens can be reliably identified to species using a combination of traits.

REMARKS: Our analyses of cytochrome-*b* sequence data recovered several robustly supported haplogroups that we regard as conspecific despite the presence of noteworthy geographic size variation (Teta et al., 2009; Voss et al., 2009). Because the collection localities of sequenced specimens of *Thylamys pusillus* are spatially clustered with large intervening areas from which no sequence data are available (fig. 7), geographic sampling bias is a possible explanation for the seemingly distinct groups in our cytochrome-*b* analyses. Nevertheless, sequence divergence among these haplogroups is impressive: 6.8% between haplogroup A and haplogroup B, 7.6% between haplogroup A and haplogroup C, and 5.8% between haplogroup B and haplogroup C. If these really are conspecific mitochondrial lineages, they are old ones. In the event that diagnostic morphological criteria are eventually found to reliably distinguish these haplogroups, we discuss the application of available names in the paragraphs that follow.

Haplogroup A, represented in our analyses by samples from southeastern Bolivia and western Paraguay, corresponds to *Thylamys pusillus* in the strict sense of Voss et al. (2009), who designated a neotype from the Paraguayan department of Boquerón; *nanus* is an objective junior synonym (based on the same type material); and *verax*, a subjective junior synonym, is also based on a western Paraguayan type (table 14). Voss et al. (2009) conjectured that typical *pusillus* might be restricted to the tropical and subtropical dry forests north of the Río Pilcomayo, from which measured specimens seem to be larger (with upper molar tooth rows > 5 mm) than specimens collected south of the Pilcomayo—in Argentina—which are mostly smaller (with tooth rows < 5 mm). However, a previously unexamined USNM series from Fortín Guachalla (22°27′S, 62°20′W) on the north bank of the Pilcomayo is geographically intermediate to the material examined by

Voss et al. (2009), and it is also morphologically intermediate (with LM = 4.9–5.3 mm), suggesting that geographic variation is clinal rather than abrupt, and that the Pilcomayo does not separate morphologically distinctive forms.

Haplogroup B, represented by geographically adjacent samples from the Argentine provinces of Catamarca and Santiago del Estero, corresponds to the small-bodied phenotype that Voss et al. (2009) associated with *bruchi*, a name that has been variously treated as a junior synonym of *Thylamys pusillus* (e.g., by Voss and Jansa, 2009) or *T. pallidior* (e.g., by Gardner, 2005). Although the type locality of *bruchi* is in the Argentine province of San Luis, from which no additional *pusillus*-like material is known to have been collected, the subadult holotype (BMNH 21.4.21.8) has all the distinguishing characteristics of *pusillus*, including short claws, an infraorbital foramen that is dorsal to P3, distinct maxillary fenestrae, a well-developed stylar cusp C on M1 and M2, and a well-developed metaconule on M3. The name *pulchellus* (based on a specimen from Santiago del Estero; table 14) also applies to this haplogroup according to Teta et al. (2009), but we have not examined the type.

Voss et al. (2009) thought that *bruchi* might be distinct from *pusillus* based on the smaller size of specimens collected south of the Pilcomayo by comparison with specimens collected in Paraguay and Bolivia, and because they observed correlated geographic variation in the frequency of stylar cusp C on M3. As discussed above, however, newly examined material suggests that geographic size variation in this complex is clinal and does not provide a satisfactory basis for identifying unsequenced specimens. Representative voucher specimens of haplogroup B are, in fact, smaller than vouchers of haplogroup A (table 17), but observed metrical differences are small, and stylar cusp C occurs polymorphically on M3 in voucher material of both haplogroups. Because close scrutiny has not revealed additional phenotypic differences between specimens that might be referred to *bruchi* on the one hand and to *pusillus* on the other, it seems appropriate to adopt the taxonomically conservative view that these are conspecific forms.

Haplogroup C represents the nominal taxon *citellus*, an identification that is convincingly established by sequence data that we obtained from a century-old paratype (BMNH 1898.8.19.12; table 1).[4] This haplogroup occurs in the so-called Mesopotamian region of Argentina (between the Paraná and Uruguay rivers), where our samples were collected in the provinces of Corrientes, Entre Ríos, and Misiones. Measured voucher material and other (unsequenced) Mesopotamian specimens are larger than *bruchi* (e.g., with LM = 5.4–5.8 mm), but they overlap broadly with typical *pusillus* (from the Chaco Boreal) in all measured craniodental dimensions and lack any distinguishing qualitative trait. Whereas several specimens from Corrientes (e.g., BMNH 98.8.19.9, 98.8.19.11, 98.8.19.12) have white-tipped tails, for example, this marking was not observed in material that we examined from Misiones.

Specimens from high elevations (> 2000 m) in the Andes of Chuquisaca department, Bolivia, that Anderson (1997: 164) identified as *Thylamys pusillus* all appear to be examples of *T. venustus*. Relevant specimens that we examined include sequenced material from "9 km by road N Padilla," "11 km N and 16 km W Padilla," "12 km N and 11 km E Tarabuco," "2 km N Tarabuco," and "4 km N Tarabuco" (see Specimens Examined in our account for *T. venustus*, below). Although some material from these localities remains unexamined, the lack of any verified high-elevation records of *T. pusillus* and the lack of accurately diagnostic couplets in Anderson's (1997: 29) key to *Thylamys* lead us to believe that none of his Andean material represents this species.

Specimens of *Thylamys pallidior* have sometimes been misidentified as *T. pusillus*, most recently by Birney et al. (1996), who reported finding two distinct phenotypes in

[4] Creighton and Gardner (2008: 114) alleged that "*marmota* Thomas, 1896" is a senior synonym of *citellus*, but Thomas's (1896) use of *marmota* Oken, 1816—an unavailable name based on Azara's fourth opossum (the Paraguayan species currently known as *Thylamys macrurus*; Voss et al., 2009)—for Argentinian material was a misidentification that he subsequently corrected (Thomas, 1912). Because Thomas (1896) was not proposing a new name, his citation of a previous description (Thomas, 1894) to clarify the application of Oken's epithet cannot be construed as a nomenclaturally valid indication in the sense of the Code (ICZN, 1999: Article 12).

TABLE 17
Measurements (mm) of Sequenced Adult Specimens of *Thylamys pusillus*[a]

	Haplogroup A		Haplogroup B		Haplogroup C	
	Males[b]	Females[c]	OMNH 23483♂	OMNH 32562♀	BMNH 98.8.19.12♀[d]	ZSM 1966/70♀
HBL	100 (93–105) 3	100 (91–116) 3	88	96	"132"	"86"
LT	118 (110–134) 3	119 (107–131) 3	98	100	"127"	"109"
HF	14 (14–15) 3	14 (13–15) 3	13	12	"15"	"14"
Ear	21 (19–25) 3	21 (19–24) 3	22	20	"25"	"22"
CBL	27.7 (27.0–28.5) 3	26.4 (25.6–27.0) 3	24.3	—	29.8	25.7
NL	11.8 (11.8) 1	11.2 (11.2) 1	—	10.2	12.4	10.7
NB	2.3 (2.1–2.7) 3	2.5 (2.0–2.9) 3	2.2	2.5	2.6	2.3
LIB	4.1 (4.0–4.2) 3	3.9 (3.6–4.3) 3	3.6	3.8	4.6	3.7
ZB	15.5 (15.0–16.1) 3	15.5 (15.2–15.9) 2	13.8	14.2	17.7	15.0
PL	14.9 (14.4–15.3) 3	14.2 (13.9–14.8) 3	13.0	13.2	15.7	14.1
PB	8.8 (8.6–9.0) 3	8.5 (8.3–8.6) 3	7.6	7.8	9.5	8.5
MTR	10.5 (10.4–10.6) 3	10.1 (9.7–10.4) 3	9.3	9.2	10.6	10.3
LM	5.5 (5.3–5.7) 3	5.3 (5.0–5.6) 3	5.0	4.8	5.5	5.4
M1–3	4.8 (4.6–5.0) 3	4.6 (4.4–4.7) 3	4.3	4.1	4.7	4.7
WM3	2.0 (1.9–2.2) 3	2.0 (1.9–2.1) 2	1.7	1.6	1.9	1.9
BW	3.1 (2.9–3.2) 3	3.0 (2.8–3.1) 3	3.1	—	3.3	—
IBW	4.3 (4.2–4.5) 3	4.3 (4.1–4.5) 3	3.5	—	4.3	—

[a]External measurements enclosed by quotes (e.g., "132") were recorded by collectors following European measurement conventions and may not be comparable to values obtained by American collectors (LT, HF, Ear) or computed from measurement values recorded by American collectors (HBL; see Materials and Methods).

[b]AMNH 275440; TTU 109052, 109099. Tabulated statistics include the sample mean, the observed range (in parentheses), and the sample size.

[c]AMNH 260025, MSB 67016, TTU 65463. Tabulated statistics include the sample mean, the observed range (in parentheses), and the sample size.

[d]An old specimen with heavily worn teeth.

material they collected in "Monte" and "Patagonian" habitats of Chubut province, Argentina. However, we examined Birney at al.'s material (in the MMNH) and found no morphological differences between their Monte and Patagonian series. The morphometric variation among adult MMNH specimens from Chubut is well within the normal range of intraspecific variation in *Thylamys*, and both series conform qualitatively to our diagnosis of *T. pallidior*.[5] No specimen in either series resembles *T. pusillus*. Unfortunately, tissue samples from Birney at al.'s Chubut material (which may still exist in a freezer at Texas Tech University; C.J. Phillips, personal commun.) could not be obtained for our sequencing study.

SPECIMENS EXAMINED ($N = 84$): **Argentina**—*Catamarca,* Bella Vista (OMNH 32562, 32563), Chumbicha (OMNH 23483), 5.2 km NW Chumbicha (OMNH 32561); *Corrientes,* Estancia Corona, near Goya (BMNH 94.6.30.1), Goya (BMNH 98.8.19.9 [holotype of *citellus*], 98.8.19.10–98.8.19.12); *Entre Ríos,* La Paz (BMNH 23.12.12.16); *Mendoza,* Ñacuñán Reserve (UWBM 72205); *Misiones,* Dos de Mayo (ZSM 1966/70–1966/74); *San Luis,* Alto Pencoso (BMNH 21.4.21.8 [holotype of *bruchi*]); *Santiago del Estero,* 6 km S and 2 km E Pampas de los Guanacos (OMNH 23479); *Tucumán,* Tapia (USNM 236332). **Bolivia**—*Chuquisaca,* 3.8 km by road E Carandaytí (AMNH

[5]Birney et al. (1996) claimed that their Monte and Patagonian series differed in pelage traits (fur color and texture) and in the position of the infraorbital foramen above the maxillary tooth row. However, three of their four Monte specimens are juveniles with obviously immature pelage; their single Monte adult (MMNH 15722) closely resembles Patagonian specimens in pelage characteristics. Apparently, the authors mistook dP3 for M1 when they recorded the position of the infraorbital foramen above the tooth row in their Monte juveniles. The position of the infraorbital foramen in MMNH 15722 is indistinguishable from the morphology seen in their Patagonian series (above stylar cusp B of M1)

TABLE 18
Morphological Comparisons among Species in the Elegans Group of *Thylamys*

	elegans	*pallidior*	*tatei*
Lateral zones of gray-based ventral fur	broad	narrow/absent	broad
White tail tip	absent	absent	usually present
Nasals	usually short	variable[a]	usually long
Lacrimal foramina	usually exposed	variable[b]	concealed
Infraorbital foramen	usually over M1	usually over M1	usually over P3
Upper second incisor (I2) crown	≤ I3 crown	≤ I3 crown	> I3 crown
Molar length (LM, mm)	5.6–6.2 mm	5.3–5.9 mm	5.9–6.4 mm

[a]See table 7.
[b]See table 8.

261268; MSB 55846); *Santa Cruz*, 53 km E of Boyuibe (AMNH 275441; MSB 87105), Tita (AMNH 260025); *Tarija*, Estancia Bolívar (AMNH 275440, 275442, 275445, 275446; MSB 67016–67018, 87103, 87104), 8 km S [and] 10 km E Villa Montes (AMNH 246442–246444, 246446–246449, 246452). **Paraguay**—*Alto Paraguay*, Destacamento Militar Gabino Mendoza (TTU-TK 65601, 65632, 65635), Fortín Pikyrenda (TTU-TK 65592, 65612), Palmar de las Islas (TTU-TK 65458, 65463); *Boquerón*, Estancia "El 43" (TTU-TK 60217, 60227), Estancia Toledo (FMNH 164097), Experimental Farm (FMNH 164095, 164096), Fortín Guachalla (FMNH 54369; USNM 390027–390033), Orloff (FMNH 63862), Parque Cué (TTU-TK 63360, 63367), Parque Nacional Teniente Agripino Enciso (TTU-TK 65031, 65104, 65215, 66463, 66468, 66469, 66476; USNM 555660), Schmidt Ranch (FMNH 164086), 410 km NW Villa Hayes (MVZ 144312, 144313), 460 km NW Villa Hayes (MVZ 144311 [neotype of *pusillus* and *nanus*]); *Chaco*, 50 km WNW Fortín Madrejon (UMMZ 124676); *Nueva Asunción*, 1 km SW km 620 [of] Trans-Chaco Road (UMMZ 176357); 19 km by road WSW km 588 [of] Trans-Chaco Road (UMMZ 176358, TWN 240, 275, 390). *Presidente Hayes*, Misión Central (BMNH 20.12.18.34 [holotype of *verax*]), 295 km NW Villa Hayes (MVZ 144310).

The Elegans Group

Members of the Elegans Group can be distinguished from all other congeneric species by their usual lack of maxillary fenestrae, and they are the only species in the subgenus *Thylamys* to have long claws (table 16). Additionally, this morphologically distinctive and molecularly well-supported clade is the only lineage of fat-tailed mouse opossums that occurs on both sides of the Andes, all of the others being restricted to the eastern side. The Elegans Group contains three currently recognized species (table 18) and one or more unnamed forms. The latter are discussed below in the Remarks section for *Thylamys pallidior*.

Thylamys elegans (Waterhouse, 1839)

SYNONYMS: ?*soricinus* Philippi, 1894.

DISTRIBUTION: As restricted by authors (Meynard et al., 2002; Solari, 2003; Braun et al., 2005; Creighton and Gardner, 2008) and as recognized in this report, *Thylamys elegans* is endemic to central Chile, where its distributional limits remain to be convincingly documented. Examined specimens that we refer to this species were collected between about 30° and 36°S (in the regions of Coquimbo, Valparaíso, Metropolitana, and Maule), from near sea level to about 1000 m. As noted by Palma (1995), the specimens reported from much lower latitudes and/or higher elevations in northern Chile (Atacama and Tarapacá) by Pine et al. (1979) are referable to *T. pallidior*. Although Creighton and Gardner (2008: 110) did not map any northern Chilean localities for *T. elegans*, the elevational range that they attributed to this species ("from sea level to over 3500 m") was presumably based on Pine et al.'s (1979) misidentified material. The type of *soricinus* is said to have been collected near Valdivia

(ca. 40°S), but no additional specimens have apparently been collected so far to the south (Palma, 1997).

Although the geographic range of *T. elegans* is not known to overlap that of any other congeneric species, newly identified material (see Remarks, below) indicates that the the range of *T. pallidior* closely approaches it in the Coquimbo region, where the two species might eventually be found to occur sympatrically.

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage narrowly self-whitish or -yellowish from chin to anus, with broad lateral zones of gray-based hairs (in specimens from Coquimbo, Metropolitana, and Valparaíso), *or* almost entirely gray-based buffy with or without self-whitish midpectoral markings (in specimens from Maule); plantar pads of manus separate, surrounding a concave central palmar surface, and with well developed dermatoglyphs; manual claws long, extending well beyond fleshy apical pads of digits; tail usually longer than combined length of head and body (LT/HBL $\times$ 100 = 108%; N = 27), without pale tip; prehensile ventral surface of tail tip well developed. Nasal bones usually short (not extending posteriorly as far as the lacrimals); lacrimal foramina usually exposed anterior to orbit or partially exposed on orbital rim; infraorbital foramen above P3/M1 commissure or above M1; nasolabial fossa shallow; supraorbital margins usually rounded or squared; maxillary fenestrae consistently absent; crown of second upper incisor (I2) smaller than or subequal to crown of I3; stylar cusp C almost always absent on M1 and M2; metaconule absent or indistinct on M3.

COMPARISONS: *Thylamys elegans* can be distinguished unambiguously from *T. pallidior* by its much broader lateral zones of gray-based ventral fur, which are equal to or wider than the median streak of self-colored fur (versus much narrower than the self-colored zone in *pallidior*). Additionally, the self-colored ventral fur of *elegans* is usually off-white ("cream") or even yellowish, whereas the self-colored ventral fur of *pallidior* is snowy white. Other characters contribute to the phenotypic distinctness of these species, although none provides a sufficient basis for identification by itself: *elegans* has, on average, larger hind feet (14–17 mm) than *pallidior* (12–15 mm), longer manual and pedal digits, shorter nasals (table 7), and less inflated auditory bullae. Digital lengths are difficult to measure (we did not attempt to do so), but the longer fingers and toes of *elegans* are apparent in most side-by-side comparisons. Bullar size is indexed by the ratio of bullar width to interbullar width (BW/IBW; see fig. 2), a proportion that averages 0.85 $\pm$ 0.05 SD (N = 23) in *elegans* and 0.98 $\pm$ 0.07 SD (N = 44) in *pallidior*.

Thylamys elegans externally resembles *T. tatei* in having wide lateral zones of gray-based ventral fur, but these species can be distinguished unambiguously by incisor morphology. Whereas the crown of I2 is consistently smaller than or subequal to the crown of I3 in *elegans*, the crown of I2 is consistently larger than the crown of I3 in *tatei* (fig. 17). Additionally, the nasals of *elegans* are usually shorter than those of *tatei* (table 7); one or both lacrimal foramina are usually exposed in *elegans*, whereas both foramina are concealed in *tatei* (table 8); and the infraorbital foramen of *elegans* is usually positioned over M1, whereas the foramen is often over P3 in *tatei* (table 9). Among the integumental differences that Solari (2003) observed between *elegans* and *tatei*, the usual presence of a pale tail tip in *tatei* and its absence in *elegans* is the most consistently useful; we did not observe conspicuous differences between these taxa in fur length (10–12 mm middorsally in most examined specimens of both species), dorsal pelage pigmentation, or facial markings.

REMARKS: The holotype of *coquimbensis* (FMNH 22302), a taxon originally described from the Coquimbo region of Chile as a subspecies of *elegans* by Tate (1931), is unambiguously referable to *Thylamys pallidior*. All of the distinctive traits of *coquimbensis* mentioned by Tate (1931, 1933)—including its pale dorsal coloration, mostly white ventral fur, small feet, and large bullae—are consistent with the diagnostic traits that we attribute to T. *pallidior*. Side-by-side comparisons of FMNH 22302 with examples of typical *T. elegans* (which also occurs in Coquimbo; e.g., FMNH 119487) are

TABLE 19
Measurements (mm) of Sequenced Adult Specimens of *Thylamys elegans*

	Coquimbo	Valparaíso		Metropolitana	
	MSB 87097♀	MSB 87098♀	MSB 133095♂	MSB 133097♀	MSB 133104♂
HBL	90	127	112	106	112
LT	120	134	118	105	110
HF	16	18	15	15	16
Ear	25	24	26	26	"18"[a]
CBL	28.6	31.4	29.5	29.0	29.6
NL	11.5	12.9	12.4	11.9	11.9
NB	2.2	2.3	2.1	2.0	2.0
LIB	4.2	4.8	4.5	4.4	4.6
ZB	15.8	17.2	15.1	15.6	15.6
PL	15.5	17.2	16.5	15.9	16.3
PB	9.1	9.8	9.1	9.3	9.2
MTR	10.7	12.0	11.8	11.4	11.9
LM	5.6	6.0	6.2	6.0	6.2
M1–3	4.9	5.2	5.2	5.0	5.2
WM3	2.0	2.2	2.1	2.1	2.1
BW	3.2	3.4	3.4	3.3	3.4
IBW	3.7	4.0	4.4	4.2	4.2

[a]We assume that this is a measurement or recording error, because the ear of this specimen does not appear to be unusually small.

likewise consistent with the suite of differences that distinguish these species (see Comparisons, above). The occurrence of both species in Coquimbo suggests that they may occur sympatrically there, perhaps somewhere in between Paiguano (30°01′S, 70°32′W; the type locality of *coquimbensis*) and Parque Nacional Fray Jorge (30°30′S, 71°30′W; our northernmost record of *T. elegans*).

We have not examined the type of *soricinus*, whose widely assumed synonymy with *elegans* still needs to be confirmed. The type of *soricinus,* a mounted skin with the skull inside, was last seen by Osgood (1943), who noted that it differed from typical *elegans* by lacking the continuous median streak of self-whitish fur seen in the latter form; instead, he described the ventral surface of the type of *soricinus* as entirely covered by gray-based buffy hairs. The only Chilean specimens we examined that fit this description are a small series from Maule (USNM 541587–541591) from which, unfortunately, we have no sequence data. Pine et al. (1979) previously examined this series and concluded that it represents the *soricinus* phenotype. We agree, but because the Maule specimens are indistinguishable from typical *elegans* in measurements and qualitative craniodental traits, no taxonomic distinction seems warranted at this time.

Measurements of sequenced adult specimens of *Thylamys elegans* are provided in table 19.

SPECIMENS EXAMINED ($N = 29$): **Chile**—*Coquimbo,* 10 km N Puente Los Molles (FMNH 119487), Fray Jorge National Park (MSB 70588, 87095, 87096, 87097); *Maule,* confluence of Río Maule and Río Claro (USNM 541587), Siete Tasas (USNM 541588–541591); *Metropolitana,* 7 road km SW Camino Rinconada (UWBM 49000, 49006, 49007, 49011, 49014), 12 road km SW Camino Rinconada (UWBM 44443–44446), Fundo El Pangue (UWBM 49059), Rinconada de Maipu (MSB 133097), San Carlos de Apoquindo (MSB 133104); *Valparaíso,* Las Hijuelas (AMNH 97752, 97753), Olmué (AMNH 97755), Palmas de Ocoa (MSB 87098), Papudo (AMNH 97754), Quebrada del Tigre (MSB 133095).

Thylamys pallidior (Thomas, 1902)

SYNONYMS: *coquimbensis* Tate, 1931; *fenestrae* Marelli, 1932.

DISTRIBUTION: As recognized in this report, *Thylamys pallidior* occurs from eastern Arequipa and Tacna departments in southwestern Peru eastward and southward into Bolivia (Oruro, Chuquisaca, Tarija) and northern Chile (Antofagasta, Atacama, Coquimbo, Tarapacá) to Argentina. In Argentina, *Thylamys pallidior* ranges from Jujuy province southward to Chubut (Flores et al., 2007). Specimens that we examined document an altitudinal range from near sea level to 3750 m. Misidentified material that has been reported from extralimital localities is discussed under Remarks (below).

The known geographic range of *Thylamys pallidior* overlaps that of *T. sponsorius* in northwestern Argentina, where the two species have been collected sympatrically near Barcena (gazetteer locality 11) in Jujuy province. The range of *T. pallidior* also overlaps that of *T. pusillus*, as described in the account of the latter species (above). Although the ranges of *T. pallidior* and *T. venustus* also overlap in northwestern Argentina, these species have apparently not been collected sympatrically. Sympatry between *T. pallidior* and *T. elegans* is to be expected in the Coquimbo region of Chile, where their known geographic ranges are closely juxtaposed (see Remarks for *T. elegans*, above).

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage entirely self-white or with narrow lateral zones of gray-based hairs; plantar pads of manus separate, surrounding concave central palmar surface, and with well-developed dermatoglyphs; manual claws long, extending well beyond the fleshy apical pads of digits; tail longer than combined length of head and body (LT/HBL $\times$ 100 = 112%; $N = 41$), without pale tip; prehensile ventral surface of tail tip well developed. Nasal bones variable in length (without any clearly modal condition; table 7); lacrimal foramina often partially exposed on orbital rim; infraorbital foramen usually above M1 but sometimes above P3/M1 commissure (apparently never above P3); nasolabial fossa shallow; supraorbital margins usually rounded or squared; maxillary fenestrae almost always absent; crown of second upper incisor (I2) consistently smaller than crown of I3; stylar cusp C almost always absent on M1 and M2; metaconule usually absent on M3.

COMPARISONS: Comparisons of *Thylamys pallidior* with *T. pusillus* and *T. elegans* are summarized in the preceding species accounts. *Thylamys pallidior* differs from the only other currently recognized species in the Elegans Group, *T. tatei*, in size and qualitative characters. Although *pallidior* is, on average, smaller than *tatei* in all measured dimensions, age-invariant molar measurements provide the best univariate index for this comparison: mean length of the upper molar row (LM, see fig. 2) is 5.7 $\pm$ 0.2 mm S.D. (observed range: 5.3–6.0 mm; $N = 51$) in *pallidior* and 6.2 $\pm$ 0.2 mm (observed range: 5.9–6.4 mm; $N = 11$) in *tatei*. Qualitatively, these species are most readily distinguished by their ventral pelage (almost completely self-white in *pallidior,* with broad lateral zones of gray-based hairs in *tatei*) and by upper incisor morphology (the crown of I2 is consistently smaller than or about the same size as the crown of I3 in *pallidior*, whereas the crown of I2 is consistently larger than the crown of I3 in *tatei*; fig. 17).

REMARKS: As previously reported by Braun et al. (2005), cytochrome-*b* sequence variation in this species is geographically structured. In particular, our results confirm those authors' discovery of two allopatric haplotype groups with distributions that are juxtaposed at or near the border between Bolivia and Argentina (fig. 5). Although this basal dichotomy is moderately well supported by nodal statistics (fig. 4), we are unable to distinguish representative voucher specimens by any morphological criterion (univariate metrical comparisons are summarized in table 20), and we therefore treat these haplogroups as conspecific. Nevertheless, names are available for each of them should future research justify their recognition as distinct taxa. In that event, *pallidior* (based on a Bolivian specimen; table 14) unambiguously applies to haplogroup A, and *fenestrae* (based on an Argentinian specimen) could be used for haplogroup B. According to Martin (2009), however, *fenestrae* is a distinct species restricted to the Argentinian provinces of Buenos Aires, Córdoba, and La Pampa. Our only tissue samples from these

TABLE 20
Measurements (mm) of Sequenced Adult Specimens of *Thylamys pallidior*[a]

	Males		Females	
	Haplogroup A[b]	Haplogroup B[c]	Haplogroup A[d]	Haplogroup B[e]
HBL	93 (87–100) 4	91 (73–103) 5	99 (97–104) 3	95 (87–103) 2
LT	112 (108–115) 4	105 (97–110) 5	112 (107–118) 3	105 (103–107) 2
HF	14 (13–15) 5	14 (13–15) 6	14 (13–15) 3	14 (13–14) 2
Ear	24 (20–28) 5	22 (20–24) 6	24 (23–25) 3	22 (22–23) 2
CBL	27.9 (26.4–30.1) 5	27.0 (25.4–28.4) 4	27.3 (26.5–27.9) 3	26.3 (25.1–27.2) 3
NL	12.0 (11.7–12.4) 2	11.2 (10.6–11.6) 3	11.2 (11.1–11.4) 3	10.7 (10.2–11.2) 3
NB	2.4 (2.2–2.5) 5	2.2 (1.9–2.6) 4	2.4 (2.2–2.5) 3	2.3 (2.1–2.6) 3
LIB	4.6 (4.4–4.8) 5	4.3 (4.1–4.6) 4	4.6 (4.5–4.7) 3	4.2 (4.1–4.4) 3
ZB	14.9 (14.0–16.5) 5	14.4 (13.6–15.2) 4	14.8 (14.6–15.2) 3	14.7 (14.4–15.0) 2
PL	15.5 (14.5–16.6) 4	14.8 (13.7–15.8) 4	14.9 (14.8–15.0) 3	14.4 (13.6–14.9) 3
PB	8.7 (8.5–9.1) 5	8.6 (8.1–9.0) 4	8.7 (8.5–9.0) 3	8.6 (8.2–8.9) 3
MTR	10.9 (10.4–11.2) 5	10.8 (10.0–11.3) 4	10.5 (10.4–10.6) 3	10.2 (9.8–10.8) 3
LM	5.7 (5.5–6.0) 5	5.7 (5.4–5.8) 4	5.3 (5.2–5.5) 3	5.5 (5.3–5.8) 3
M1–3	4.9 (4.6–5.0) 5	4.9 (4.8–5.0) 4	4.6 (4.5–4.8) 3	4.8 (4.6–5.1) 3
WM3	2.0 (1.9–2.0) 4	2.0 (2.0–2.1) 4	2.0 (2.0–2.1) 3	2.0 (2.0–2.1) 3
BW	3.4 (3.1–3.6) 4	3.2 (2.9–3.4) 4	3.2 (3.1–3.2) 3	3.3 (3.2–3.4) 3
IBW	3.5 (3.2–3.7) 4	3.5 (3.4–3.6) 4	3.5 (3.4–3.7) 3	3.4 (3.1–3.5) 3

[a]Tabulated sample statistics include the mean, the observed range (in parentheses) and the sample size.
[b]FMNH 162495; MSB 57003, 133108; MVZ 115634, 173937.
[c]OMNH 23489, 29963, 29964, 32544, 32556, 32571.
[d]MSB 87099; MVZ 143696, 145531.
[e]OMNH 23480, 23490, 29957.

areas (AC 47, LTU 77) are vouchered by morphological specimens that we have not examined, but the sequences we obtained from them are intermingled in our tree (fig. 4) with sequences from specimens collected in other provinces. Although we have not examined any of the morphological material that Martin (2009) referred to *fenestrae*, our results suggest that the application of this name merits closer scrutiny.

Specimens of other *Thylamys* species have sometimes been misidentified as *T. pallidior*. For example, Anderson's (1997: 29) key does not reliably distinguish *T. pallidior* from other Bolivian congeners, and his range maps include several records that fall outside the range of that species as we recognize it. Although we were not able to see every Bolivian specimen that Anderson identified as *T. pallidior*, all of those that we examined from the departments of Cochabamba (e.g., AMNH 275427, MSB 87109), La Paz (e.g., AMNH 248704), and Santa Cruz (e.g., AMNH 260030) are unambiguously referable to *T. venustus* (see below).

Among the Peruvian specimens that Solari (2003) referred to *Thylamys pallidior* (and which were mapped as such by Brown, 2004: fig. 87) are several that appear to represent undescribed taxa (table 1). Some of these (e.g., MVZ 116614; from 3 mi W Atico in Arequipa department; fig. 5, locality 98) are morphologically similar to *pallidior* (with mostly self-white underparts), whereas others (e.g., MVZ 137585; from Lima department; fig. 5, locality 103) differ from typical *pallidior* by having broad lateral zones of gray-based hairs bordering a narrower median streak of self-white fur. Cytochrome-*b* sequences that we amplified from museum skins of these and other unidentified specimens from southwestern Peru are highly divergent from *pallidior* and form a monophyletic group with two sequences of *T. tatei* (fig. 4). Indeed, one of these specimens (MVZ 119913; also from Lima department; fig. 5, locality 102) resembles *tatei* and differs from other (more *pallidior*-like) Peruvian specimens by having a white-tipped tail and very long nasal bones. Although these results are

hard to interpret taxonomically with the sparse material at hand, they do suggest that the systematics of Peruvian *Thylamys* is likely to reward further study. Other researchers are currently working on this problem using freshly collected material (E. Palma, personal commun.), and we await their results with the greatest interest.

SPECIMENS EXAMINED (N = 69): **Argentina**—*Catamarca,* 17 km N Barranca Larga (OMNH 29964), 34.6 km by road W Fiambala (OMNH 34903), 7 km SW Los Morteros (OMNH 32556); *Chubut,* ca. 208 km W Dolavon (MMNH 15709, 15712–15714), Estancia La Escondida (MMNH 17323, 17324, 17366), Istmoameghino (MMNH 15722); *Jujuy,* 9 km NW Barcena (OMNH 29963), 11 km E Humahuaca and 2 km E Pucará on road to Cianzo (OMNH 29957), 8.2 km S Sey (OMNH 34911); *Mendoza,* Ñacuñán Reserve (UWBM 72195), 49.2 road km N Mendoza (UWBM 72224); 3 km W Refugio Militar General Alvarado (OMNH 23482), Salinas del Diamante RR Station (OMNH 23480); *Neuquén,* 16 km SE La Rinconada (MVZ 163772); *Río Negro,* General Roca (USNM 236331); *Salta,* 16 km S and 1.8 km W Barrancas along Río de las Burras (OMNH 34908, 34909), 17 km NW Cachi (OMNH 32559), Los Sauces (OMNH 32544); *San Juan,* Castaño Nuevo (OMNH 23485), 8 km W Complejo Astronómico El Leoncito (OMNH 32571), Quebrada de los Flores (OMNH 29961, 29962); *San Luis,* 7 km E San Francisco del Monte de Oro (OMNH 23489), 12 km by road N Varela (OMNH 23490), 15 km E Salinas del Bebedero (OMNH 23488); *Tucumán,* Tafí del Valle (AMNH 41723–41727; FMNH 41397, 41398). **Bolivia**—*Chuquisaca,* 68 km by road N Camargo (AMNH 262405–262407, MSB 57003); *Oruro,* Challapata (BMNH 2.2.2.116 [holotype of *pallidior*], USNM 121157), ca. 10 km by road SW Pazña (UMMZ 155830, 155831, 156015); *Tarija,* 1 km E Iscayachi (AMNH 262408), 2 km SE Cieneguillas (FMNH 162495), Serranía Sama (MSB 87099). **Chile**—*Antofagasta,* Muelle de Piedra E of Taltal (AMNH 143240); *Atacama,* Altamira (USNM 391776), El Transito (USNM 391775); *Coquimbo,* Paiguano (FMNH 22302 [holotype of *coquimbensis*]); *Tarapacá,* 5 km S Belén (USNM 541600), 1 km W Belén (USNM 541595, 541596), Camarones Valley (USNM 391777), Chapiquiña (USNM 541599), Enquelga (MSB 133108), 7 km SE Socorama (USNM 541593, 541594). **Peru**—*Arequipa,* 1 km N Chivay (MVZ 173937–173939), 3 mi N Mollendo (MVZ 145531); *Tacna,* 1.5 mi N Tarata (MVZ 139215), 4 km N Tarata (MVZ 115634), 65 km W Tacna (MVZ 143695, 143696).

Thylamys tatei (Handley, 1957)

SYNONYMS: None.

DISTRIBUTION: According to Solari (2003), who examined more material than we have seen, *Thylamys tatei* is known only from the Peruvian department of Ancash and from the Lomas de Lachay in the northern part of the department of Lima, between 300 and 3000 m above sea level. This species is not known to occur sympatrically with any other congener.

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage with narrowly continuous median streak of self-white (or whitish) fur from chin to anus, flanked by broad lateral zones of gray-based hairs; plantar pads of manus separate, surrounding a concave central palmar surface, and with well-developed dermatoglyphs; manual claws long, extending well beyond fleshy apical pads of digits; tail longer than combined length of head and body (LT/HBL × 100 = 113%; N = 9), usually with pale tip (whitish above and below for distal 2–18 mm); prehensile ventral surface of tail tip well developed. Nasal bones usually very long, extending posteriorly well behind lacrimals; lacrimal foramina concealed from lateral view inside orbit; infraorbital foramen above P3 or above P3/M1 commissure; nasolabial fossa shallow; supraorbital margins almost always rounded or squared; maxillary fenestrae almost always absent; unworn crown of second upper incisor (I2) consistently larger than crown of I3; stylar cusp C variably present or absent on M1, usually absent or indistinct on M2; metaconule absent on M3.

COMPARISONS: Comparisons between *Thylamys tatei* and other currently recognized species of the Elegans Group are provided in the preceding accounts. Mea-

TABLE 21
Measurements (mm) of Sequenced Specimens of *Thylamys* sp. and *T. tatei* from Peru[a]

	Thylamys sp.				*Thylamys tatei* (Ancash)	
	Arequipa	Ayacucho	Lima			
	116614♂	137896♂	119913♂	137585♂	135503♂	135504♀
Age	adult	adult	subadult	adult	adult	adult
HBL	80	91	98	98	—	109
LT	101	107	107	110	—	118
HF	14	15	16	15	16	15
Ear	21	22	24	23	21	24
CBL	25.6	—	28.0	27.4	30.7	31.4
NL	11.2	—	12.1	—	—	—
NB	2.3	2.7	2.4	2.5	2.3	2.8
LIB	4.5	4.5	4.6	4.6	4.8	4.9
ZB	13.5	13.8	14.8	14.6	16.0	17.5
PL	14.2	—	15.3	15.2	17.2	17.1
PB	8.2	8.5[b]	9.0	8.8	9.5	9.8
MTR	10.4	10.6	11.4	11.0	12.1	11.8
LM	5.6	5.7	6.0	5.9	6.4	5.9
M1–3	4.9	5.0	5.2	4.9	5.5	4.9
WM3	2.0	2.0	2.2	2.1	2.3	2.2
BW	3.3	3.2	3.4	3.4	3.8	3.1
IBW	3.3	3.6	4.1	3.9	4.0	4.3

[a]All specimens from MVZ.
[b]Estimated value.

surement data from sequenced specimens of *T. tatei* and specimens of related but unnamed forms from the Peruvian departments of Arequipa, Ayacucho, and Lima are provided in table 21.

REMARKS: Originally described as a valid species, *tatei* was subsequently listed as a synonym of *Thylamys elegans* by Gardner (1993). Although our results are obviously consistent with recent inferences from molecular and morphological studies that *tatei* and *elegans* are distinct species (Meynard et al., 2002; Palma et al., 2002; Solari, 2003; Braun et al., 2005), other taxonomic problems remain. Foremost among these is the identification of specimens from the Peruvian provinces of Lima (e.g., MVZ 119913, 137585) and Huancavelica (e.g., MVZ 136249) that resemble *tatei* in having broad lateral zones of gray-based ventral fur but which lack some of the diagnostic craniodental traits of *tatei* and have divergent mtDNA sequences. Although Solari (2003) identified these as *pallidior* (as discussed above), they cluster with *tatei* in our phylogenetic analyses.

SPECIMENS EXAMINED (N = 13): **Peru**—*Ancash,* Chasquitambo (USNM 302915 [holotype], 302916), Huaráz (FMNH 81443), 1 km N and 12 km E Pariacoto (MVZ 155503–135512).

The Venustus Group

The species that we assign to this group are from the eastern Andean slopes and foothills of Bolivia and northwestern Argentina. They can be distinguished from other members of the subgenus *Thylamys* by their relatively long tails (>130% of HBL, on average), short manual claws (never projecting much if at all beyond the fleshy apical pad on each digit), and predominantly gray-based ventral fur (with exceptions as noted below); additionally, the nasals usually project posteriorly beyond the lacrimals, maxillary fenestrae are almost always present, stylar cusp C is usually absent or indistinct, and metaconules are never well developed (table 16).

Voucher specimens representing two robustly monophyletic and highly divergent

cytochrome-*b* clades (labeled as *Thylamys sponsorius* and *T. venustus* in fig. 8) exhibit the morphological characteristics of the Venustus Group as described above. Unfortunately, sequenced specimens representing these clades are impossible to distinguish by qualitative morphological criteria. Therefore, morphometric data provide the only phenotypic basis for taxonomic identifications.

Examined voucher material representing these mtDNA clades differ visibly in average size. The clade with larger specimens, which include a sequenced topotype of *janetta*, occurs in the Bolivian department of Tarija and in the Argentine provinces of Catamarca, Jujuy, Salta, and Tucumán. The clade with smaller specimens occurs in the Bolivian departments of Chuquisaca, Cochabamba, La Paz, Santa Cruz, and Tarija, and it also occurs in the Argentinian provinces of Jujuy and Tucumán. Although the observed size difference is statistically significant in most univariate comparisons (e.g., using two-tailed *t*-tests), no single measurement is sufficient for clade identification due to overlapping variation.

Instead, we used multivariate discriminant analysis of craniodental measurements obtained from sequenced voucher material to associate nomenclaturally relevant unsequenced specimens with these mtDNA clades as follows. To maximize our sample size of sequenced specimens with complete measurement data we eliminated one measurement with several missing values (LN), and to minimize geometric bias we eliminated two out of three measurements (MTR, LM, M1–M3) that share anatomical endpoints and redundantly sample the same anteroposterior axis of dental variation (fig. 2). We $\log_e$-transformed our data and computed a Fisherian discriminant function from the pooled variance-covariance matrix using the *lda* command (Venables and Ripley, 1999) as implemented in R version 2.8.0 (R Development Core Team, 2008).

The results of this analysis (tables 22, 23; fig. 18) unambiguously associate the holotype of *sponsorius* with the "large" clade, which also contains a sequenced topotype of *janetta*; of these two available names, *sponsorius* is the older epithet (table 14). By contrast, the holotype of *cinderella* and a paratype of *venustus* are unambiguously assignable to the "small" clade; of these synonyms, *venustus* is the older name. Our morphometric results make biogeographic sense because the relevant type localities fall within the known range limits of the mtDNA clades to which these names apply. In particular, the type locality of *venustus* is in the Bolivian department of Cochabamba (table 14), where only the "small" clade is known to occur.

Despite some misgivings about morphometric intermediates (e.g., FMNH 162505, OMNH 29966; fig. 18) and the lack of any other diagnostic criterion, we provisionally regard *Thylamys sponsorius* and *T. venustus* as valid species. Although this conclusion does not follow from the operational criteria for species recognition suggested in our Introduction, reproductive isolation seems to be the only plausible explanation for the existence of two genetically and phenotypically divergent groups with broadly overlapping geographic distributions. Other complexities of species recognition and nomenclature are discussed in the following accounts.

Thylamys sponsorius (Thomas, 1921)

SYNONYMS: *janetta* Thomas, 1926.

DISTRIBUTION: Based on specimens that we sequenced, *Thylamys sponsorius* occurs along the eastern slopes and foothills of the Andes from southern Bolivia (Tarija) to northwestern Argentina (Jujuy, Salta, Tucumán, Catamarca; fig. 9) with recorded elevations ranging from 515 to 3750 m. Although *T. sponsorius* and *T. venustus* have broadly overlapping horizontal and vertical distributions, our only sympatric samples are from 3 km SE Cuyambuyo, at 900 m elevation in the Bolivian department of Tarija (fig. 9, gazetteer locality 74). The known geographic range of *Thylamys sponsorius* also overlaps that of *T. pallidior* as previously described in the account of the latter species (above).

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler lateral coloration present); ventral pelage gray-based yellowish or whitish, except in some old adults from

TABLE 22
Results of Linear Discriminant Analysis of Sequenced Venustus Group Specimens and Three Unknowns[a]

			Probability of assignment to	
Catalog #	MtDNA clade	Score	Large clade	Small clade
MSB 87107	small	4.05	0.00	1.00
MSB 67008	small	3.40	0.00	1.00
AMNH 261264	small	3.15	0.00	1.00
MSB 67007	small	2.71	0.00	1.00
AMNH 275427	small	2.28	0.00	1.00
AMNH 263558	small	2.13	0.00	1.00
MSB 87100	small	2.11	0.00	1.00
MSB 63264	small	1.98	0.00	1.00
MSB 63269	small	1.86	0.00	1.00
BMNH 0.7.9.20[b]	unknown	1.81	0.00	1.00
MSB 67005	small	1.80	0.00	1.00
AMNH 261245	small	1.79	0.00	1.00
AMNH 275429	small	1.40	0.00	1.00
AMNH 261255	small	1.38	0.00	1.00
AMNH 261260	small	1.19	0.00	1.00
MSB 67392	small	0.82	0.00	1.00
AMNH 275433	small	0.74	0.00	1.00
AMNH 261254	small	0.63	0.01	0.99
AMNH 260030	small	0.58	0.01	0.99
OMNH 29976	small	0.46	0.02	0.98
BMNH 2.1.1.119[c]	unknown	0.41	0.02	0.98
MSB 63262	small	0.39	0.02	0.98
MSB 63260	small	0.19	0.04	0.96
OMNH 29966	small	−0.40	0.34	0.66
FMNH 162505	large	−0.56	0.50	0.50
OMNH 29977	large	−1.60	0.99	0.01
UMMZ 155836[d]	large	−1.91	1.00	0.00
OMNH 29965	large	−1.96	1.00	0.00
MSB 67012	large	−2.41	1.00	0.00
MSB 67010	large	−2.44	1.00	0.00
AMNH 275437	large	−2.59	1.00	0.00
OMNH 34534	large	−2.71	1.00	0.00
OMNH 29974	large	−2.85	1.00	0.00
MSB 67015	large	−2.85	1.00	0.00
MSB 67014	large	−3.05	1.00	0.00
OMNH 29967	large	−3.11	1.00	0.00
OMNH 29970	large	−3.23	1.00	0.00
OMNH 32545	large	−3.38	1.00	0.00
BMNH 21.1.1.85[e]	unknown	−3.73	1.00	0.00

[a]See text.
[b]Holotype of *cinderella*.
[c]Paratype of *venustus*.
[d]Topotype of *janetta*.
[e]Holotype of *sponsorius*.

Carlazo, Bolivia (type series and topotypes of *"janetta"*), which have mostly self-whitish venters; plantar pads of manus separate, surrounding a concave central palmar surface; manual claws short, not extending much if at all beyond fleshy apical pads of digits; tail substantially longer than the combined length of head and body (LT/HBL × 100 = 136%; $N = 13$), without pale tip; prehensile ventral surface of tail tip well developed.

TABLE 23
Coefficients of Linear Discriminant Function Separating *Thylamys sponsorius* from *T. venustus*

Variable	Coefficient
$\log_e$ CBL	−16.871318
$\log_e$ NB	−2.034895
$\log_e$ LIB	−15.125179
$\log_e$ ZB	−12.330177
$\log_e$ PL	2.227723
$\log_e$ PB	13.869949
$\log_e$ LM	−39.388257
$\log_e$ WM3	−8.650411
$\log_e$ BW	17.681633
$\log_e$ IBW	9.845243

Nasal bones usually extending posteriorly as far as or behind lacrimals; lacrimal foramina usually concealed or only partially exposed on orbital rim; infraorbital foramen often over P3/M1 commissure, but sometimes over P3 or M1; nasolabial fossa shallow; supraorbital margins rounded or squared, with weak beads in some old adults but apparently never with distinct processes; maxillary fenestrae consistently present; crown of second upper incisor (I2) consistently smaller than or subequal to crown of I3; stylar cusp C almost always absent on M1 and M2; metaconule indistinct or absent on M3.

COMPARISONS: Sequenced material of *Thylamys sponsorius* seems to be indistinguishable from that of *T. venustus* in external morphological characters. Voucher specimens of both clades have brownish-gray dorsal fur that tends to be darker at lower elevations and paler in the highlands (>2000 m). The ventral fur is predominantly gray based in most specimens, although the fur of the chin and throat is often self-colored, and many specimens of both species have self-colored pectoral markings; the self-colored ventral fur (if any) and the tips of the gray-based ventral hairs are white or off-white (cream) in most highland specimens but yellowish in lowland material. The hind feet of *T. sponsorius* seem a little darker, on average, than those of *T. venustus*, but the difference is not sufficiently marked to sort skins, and it is probably useless for field identification.

Sequenced specimens of *Thylamys sponsorius* and *T. venustus* are likewise indistinguishable by any qualitative craniodental character that we examined, nor are they consistently diagnosable by any combination of qualitative craniodental traits. Tests for craniodental trait frequency differences (as recorded in tables 7–13) are statistically significant only for the presence/absence of stylar cusp C, which is not present on M2 in any sequenced specimen of *sponsorius*, but which occurs on that tooth in a substantial number of sequenced specimens of *venustus* (table 12; $p < 0.01$ by Fisher's exact test). Among traits that we did not formally score for statistical analysis, small postorbital processes were observed on several sequenced specimens of *venustus* (e.g., AMNH 186948; MSB 63260, 67005) but not on any sequenced specimen of *sponsorius*.

Sequenced adult specimens of *Thylamys sponsorius* and *T. venustus* differ significantly in most measured dimensions. Two-tailed *t*-tests for species differences among males, the sex most abundantly represented among our adult tissue vouchers, are significant at the 5% level for all measurements except HBL, Ear, NL, BW, and IBW (table 24). In every case where a significant difference was found, *sponsorius* is the larger species. Unfortunately, observed ranges of the two species overlap for every measurement, so none is diagnostic. In the absence of other criteria, provisional identifications of unsequenced specimens can be based on discriminant scores (computed as the dot product of the coefficients in table 23 and $\log_e$-transformed craniodental measurement values). If our hypothesis of species status for these clades is correct, then the scores of unsequenced specimens (of which several hundred are preserved in museum collections) should have a distinctly bimodal distribution.

REMARKS: This taxon was originally described as *Marmosa elegans sponsoria*, but Tate (1933) treated *sponsoria* as a subspecies of *M. venusta*, and Cabrera (1958) synonymized it with *M. e. cinderella*. Gardner (1993) listed *cinderella*, *sponsorius*, and *venustus* as synonyms of *Thylamys elegans*, but allozyme data reported by Palma and Yates (1998) suggested that *venustus*—the name they used for Bolivian populations of "*elegans*" (sensu

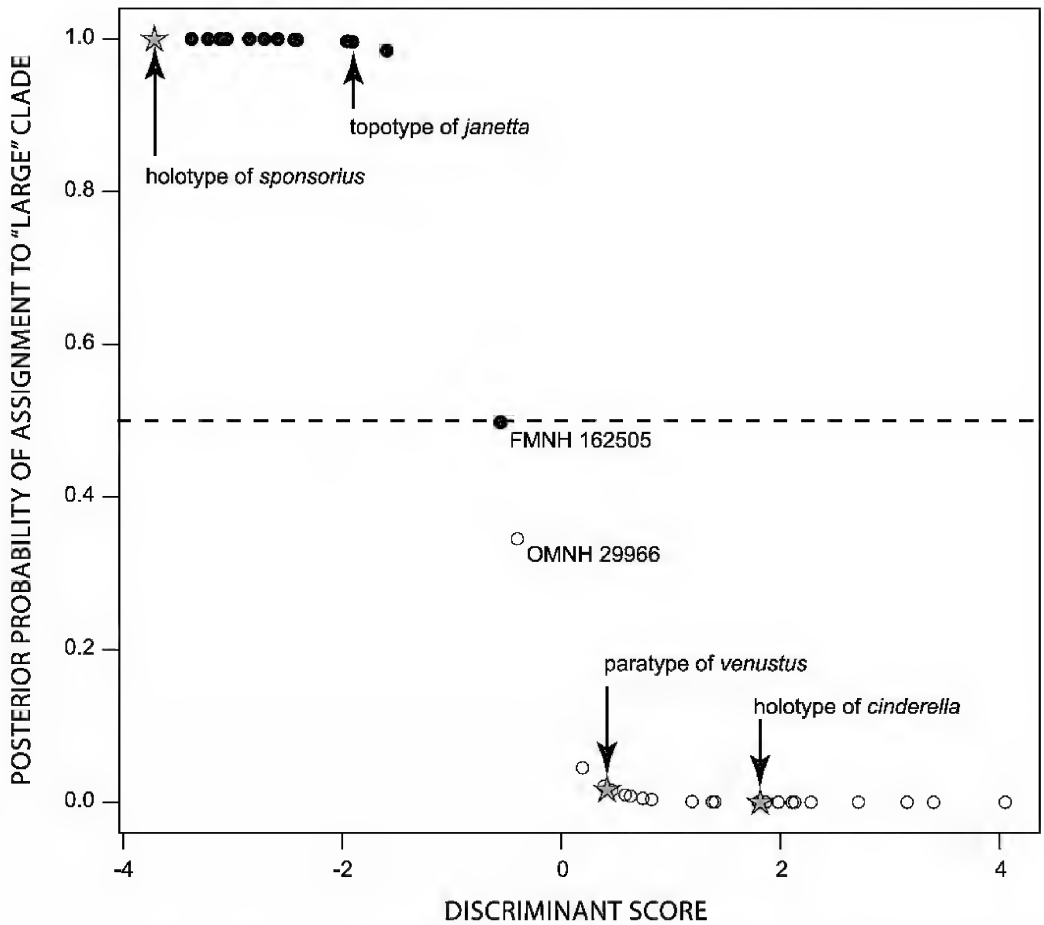

Fig. 18. Results of linear discriminant function analysis of craniodental measurement data from sequenced specimens of the Venustus Group belonging to the "large" (●) and "small" (○) clades. Unsequenced specimens (gray stars) were treated as unknowns (see table 22). Two specimens of known clade membership but with equivocal posterior probabilities are labeled with their museum catalog numbers.

Gardner, 1993)—was a distinct species. Subsequently, Flores et al. (2000) recognized three Argentine species of *Thylamys* with gray-based ventral fur, for which they used *T. cinderella*, *T. sponsorius*, and *T. venustus* as valid binomials. However, *cinderella* and *sponsorius* were synonymized again by Braun et al. (2005), who found genetic evidence for only two Argentine species of *Thylamys* with gray-based ventral fur, one corresponding to the phenotype that Flores et al. called *venustus* and the other containing specimens that Flores et al. had identified as *cinderella* and *sponsorius*. Gardner (2005) and Creighton and Gardner (2008) recognized *T. cinderella*, *T. sponsorius*, and *T. venustus* (including *janetta*) as valid following Flores et al. (2000), but Voss and Jansa (2009) followed Braun et al. (2005) in recognizing only *T. cinderella* (including *sponsorius*) and *T. venustus* (including *janetta*) as valid species.

Our use of the name *sponsorius* is based on the morphometric analysis described above, which unambiguously associates the holotype (BMNH 21.1.1.85, an adult male from Sunchal, in the Sierra de Santa Bárbara of southeastern Jujuy, Argentina; Thomas, 1921) with the cytochrome-*b* clade that has larger average measurements. Because the

TABLE 24
Measurements (mm) of Sequenced Adult Specimens of *Thylamys sponsorius and T. venustus*[a]

	Males		Females	
	sponsorius[b]	*venustus*[c]	*sponsorius*[d]	*venustus*[e]
HBL	99 (89–119) 9	96 (84–110) 17	105 (86–119) 5	90 (85–97) 3
LT	138 (129–145) 9	126 (111–138) 17	138 (125–154) 4	122 (115–125) 3
HF	17 (16–18) 9	15 (14–18) 18	17 (16–18) 5	14 (14–15) 3
Ear	24 (22–29) 9	23 (20–27) 17	24 (22–26) 5	21 (21–22) 3
CBL	29.0 (27.8–31.6) 9	27.6 (26.2–29.9) 19	29.1 (27.8–30.7) 5	26.4 (26.2–26.4) 3
NL	12.6 (11.9–13.1) 6	12.0 (11.3–13.3) 15	12.3 (11.8–12.7) 4	11.4 (11.3–11.7) 3
NB	2.6 (2.3–2.9) 9	2.4 (2.0–2.7) 19	2.7 (2.3–3.0) 5	2.2 (2.1–2.4) 3
LIB	4.7 (4.5–5.0) 9	4.3 (4.0–4.6) 19	4.6 (4.4–4.6) 5	4.2 (4.1–4.3) 3
ZB	15.8 (15.2–17.8) 9	15.0 (14.3–16.4) 19	15.8 (14.7–17.1) 5	14.1 (13.5–14.4) 3
PL	15.8 (15.3–16.6) 9	15.1 (14.4–16.4) 19	16.0 (15.5–16.5) 5	14.5 (14.4–14.7) 3
PB	9.2 (8.8–10.0) 9	8.9 (8.4–9.6) 19	9.3 (8.9–10.0) 5	8.6 (8.5–8.6) 3
MTR	11.5 (11.2–12.2) 9	10.9 (10.4–11.5) 19	11.5 (11.3–11.7) 5	10.7 (10.6–10.9) 3
LM	6.1 (5.8–6.3) 9	5.8 (5.6–6.1) 19	6.2 (6.0–6.2) 5	5.8 (5.6–5.8) 3
M1–3	5.2 (5.0–5.5) 9	5.0 (4.8–5.3) 19	5.3 (5.2–5.4) 5	4.9 (4.8–5.1) 3
WM3	2.1 (2.1–2.2) 9	2.1 (1.9–2.2) 19	2.2 (2.1–2.3) 5	2.1 (2.0–2.2) 3
BW	3.2 (2.9–3.5) 9	3.1 (2.9–3.4) 19	3.2 (2.9–3.4) 5	3.0 (3.0) 3
IBW	4.4 (4.2–4.8) 9	4.2 (3.8–4.6) 19	4.5 (4.3–4.7) 5	4.0 (3.8–4.2) 3

[a]Tabulated sample statistics include the mean, the observed range (in parentheses) and the sample size.
[b]AMNH 275437; FMNH 162505; MSB 67010, 67014; OMNH 29967, 29974, 29977, 32545; UMMZ 155836.
[c]AMNH 260030, 261245, 261254, 261260, 261264, 275427, 275429, 275433; MSB 63260, 63262, 63264, 63269, 67005, 67007, 67008, 67392, 87107; OMNH 29966, 29976.
[d]MSB 67012, 67015; OMNH 29965, 29970, 34534.
[e]AMNH 263558, 261255; MSB 87100.

same analysis assigned the holotype of *cinderella* (BMNH 0.7.9.20, an adult female from "Tucuman," Argentina; Thomas, 1902) to the clade with smaller average measurements, we conclude that these names are not synonymous. Instead, the only synonym of *sponsorius* that we are currently able to identify as such is a Bolivian form (*janetta*) whose relationships have long been controversial.

Marmosa janetta was originally described on the basis of 12 specimens collected at elevations ranging from 1700 to 2300 m in Tarija department, Bolivia, by Thomas (1926), who thought it was related to *M. verax* (a junior synonym of *Thylamys pusillus*; see above). Tate (1933: 221) also recognized *M. janetta* as a valid species and said that it was "the mountain representative of the *marmota* radiation" (*marmota* being an unavailable synonym of *T. macrurus*; see Voss et al., 2009). Subsequently, Cabrera (1958) included *janetta* without comment in the synonymy of *M. elegans venusta*. Most subsequent authors (e.g., Solari, 2003; Gardner, 2005; Creighton and Gardner, 2008) have listed *janetta* as a synonym of *T. venustus*, but the justification for this synonymy has never been explained.

We examined the holotype of *janetta* (BMNH 26.1.1.167, from Carlazo), several topotypic paratypes (BMNH 26.1.1.166, 26.1.1.168–26.1.1.170; FMNH 29169, 29170) and several recently collected topotypes (UMMZ 155836, 156034–156036). Oddly, all of these specimens are very old adults with heavily worn molars. The advanced age of these specimens plausibly explains the large size attributed to *janetta* by Thomas (1926) and Tate (1933); this conclusion is supported by the fact that whereas continuously growing dimensions seem unusually large in this series (e.g., CBL: 29.7–31.6 mm), age-invariant measurements do not (e.g., LM: 5.7–6.0 mm). Other distinctive attributes of this nominal species, however, are harder to explain as age-related, including its mostly self-white ventral coloration, white hind feet,

and short posterolateral palatal foramina (which, unlike most other *Thylamys*, do not extend anteriorly to the level of the protocone of M4). In other respects, *janetta* resembles other forms that we assign to the Venustus Group; for example, the type and all examined topotypes have short claws, and maxillary fenestrae are bilaterally present.

Our primary justification for synonymizing *janetta* with *sponsorius* are partial (609–812 bp) cytochrome-*b* sequences amplified from a paratype (FMNH 29170) and a topotype (UMMZ 155836) of *janetta*. Despite the unusual features of their morphological vouchers (as noted above), the sequences we obtained from FMNH 29170 and UMMZ 155836 cluster with other Tarija sequences that we obtained from phenotypically *sponsorius*-like specimens (fig. 8). Although we are not able to confidently explain all of the odd traits that characterize examined specimens from Carlazo, we assume that they are ontogenetic artifacts and/or local peculiarities, perhaps of a small and closely inbred population.

Flores et al. (2000, 2007) recognized *Thylamys cinderella*, *T. sponsorius*, and *T. venustus* as distinct species that could be identified by diagnostic morphometric and qualitative criteria. However, none of their relevant key couplets (Flores et al., 2000: 334) accurately distinguish voucher specimens representing the two mitochondrial clades recovered in our analysis of cytochrome-*b* sequence data. Additionally, we sequenced one specimen that they identified as *T. sponsorius* (AMNH 185323) and another that they identified as *T. cinderella* (AMNH 186948); according to our phylogenetic analyses, both specimens belong to haplogroup C of the species we identify as *T. venustus*.

SPECIMENS EXAMINED ($N = 29$): **Argentina**—*Catamarca,* 5 km S Las Higuerillas on Hwy 9 (OMNH 29965); *Jujuy,* 9 km NW Barcena (OMNH 29974), 24.8 km E Santa Clara (OMNH 34534), 10 km W Tiraxi on Hwy 29 (OMNH 29970); *Salta,* 5 km NW Pulares (OMNH 32545), 25 km SE La Viña (OMNH 32548); *Tucumán,* 5 km N Las Higuerillas on Hwy 308 (OMNH 29967), Km 42 on Hwy 364 S of San Pedro de Colalao (OMNH 32566), 7 km W Ibatín (OMNH 29977), 5 km SW Siambón (OMNH 32553). **Bolivia**—*Tarija,* Carlazo (BMNH 26.1.1.166, 26.1.1.167 [type of *janetta*], 26.1.1.168–26.1.1.170; FMNH 29169, 29170; UMMZ 155836, 156034–156036), Chuquiaca (FMNH 162505), 3 km SE Cuyambuyo (MSB 67014, 67015), 5 km NNW Entre Ríos (AMNH 275437; MSB 67010, 67012), ca. 10 km by road W Narvaez (FMNH 162507), 1 km E Tucumilla (MSB 67009).

Thylamys venustus (Thomas, 1902)

SYNONYMS: *cinderella* Thomas, 1902.

DISTRIBUTION: Based on specimens that we sequenced, *Thylamys venustus* occurs along the eastern slopes and foothills of the Andes from Bolivia (Cochabamba, Chuquisaca, Santa Cruz, and Tarija) to northwestern Argentina (Jujuy and Tucumán; fig. 9) with recorded elevations ranging from about 350 to 4000 m above sea level. Although we have not investigated every published extralimital record of this species, those from Lima, Peru (Tate, 1933) and Oruro, Bolivia (Anderson, 1997) appear to be based on misidentified material (see Remarks). Gardner's (2005) record from Neuquén, Argentina, was based on an editing error (A.L. Gardner, in litt., 23 February 2010).

The known geographic range of *Thylamys venustus* overlaps those of *T. pallidior, T. pusillus*, and *T. sponsorius*; known cases of sympatry among these species have already been described in preceding accounts.

MORPHOLOGICAL DIAGNOSIS: Body pelage tricolored (abrupt line of transition from darker middorsal to paler dorsolateral coloration present); ventral pelage gray-based yellowish or whitish; plantar pads of manus separate, surrounding a convex central palmar surface; manual claws short, not extending much if at all beyond fleshy apical pads of digits; tail substantially longer than the combined length of head and body (LT/HBL $\times$ 100 = 131%; $N = 21$), without pale tip; prehensile ventral surface of tail tip well developed. Nasal bones usually extending posteriorly as far as or behind lacrimals; lacrimal foramina variable in position (no unambiguously modal condition observed among sequenced specimens); infraorbital foramen usually above P3 or above P3/M1 commissure; nasolabial fossa shallow; supra-

orbital margins usually rounded or squared, sometimes produced as small postorbital processes; maxillary fenestrae almost always present bilaterally; crown of second upper incisor (I2) consistently smaller than or subequal to crown of I3; stylar cusp C variably present or absent on M1 and M2, but seldom a discrete, well-developed structure (usually partially fused with stylar cusp D); metaconule usually absent on M3.

COMPARISONS: See the preceding species account for morphological comparisons between *Thylamys venustus* and *T. sponsorius*.

REMARKS: Diligent visual and morphometric comparisons of voucher material has not allowed us to discover any phenotypic attribute that distinguishes the three allopatric haplogroups of *Thylamys venustus* designated A, B, and C in figures 8 and 10. The skins, skulls, and dentitions assignable to those groups are qualitatively similar and overlap broadly in all recorded measurements. In effect, they appear to represent a single morphological species. Despite the apparent absence of diagnostic morphological traits, however, available names can tentatively be assigned to two of them based on geographic criteria: the type locality of *venustus* (in the Bolivian department of Cochabamba; table 14) falls within the known range of the haplogroup A, whereas the type locality of *cinderella* (in the Argentinian province of Tucumán) falls within the known range of haplogroup C. Apparently, no name is currently available for haplogroup B.

We examined one of the two specimens that Tate (1933: 225) identified as *Marmosa venusta* from the Peruvian department of Lima, on the wrong (western) side of the Andes and over 1000 km from the nearest collection locality of any material conforming to *T. venustus* as recognized herein. The specimen in question (FMNH 24141), a juvenile male skin and skull collected in 1922 by J.T. Zimmer at Matucana (11°51′S, 76°24′W, 2378 m; Stephens and Traylor, 1983), has a relatively short tail (108% of HBL), long claws, and a narrow but continuous median streak of self-white ventral fur flanked by broad lateral zones of gray-based hairs, traits that better match the characteristics we associate with the Elegans Group than those we associate with the Venustus Group (table 16). Solari (2003) examined this specimen and identified it as *T. pallidior*, but we believe it to represent one of the unnamed phenotypes related to *T. tatei*, as discussed above in the account for the latter species.

Three specimens from the Bolivian department of Oruro that Anderson (1997) identified as *Thylamys venustus* are the only examples reported from the altiplano, where only *T. pallidior* is known to occur. Although Anderson did not publish the museum catalog numbers of the material he examined, his card files (in the AMNH Department of Mammalogy archives) identify the Oruro specimens as CM 5227, MVZ 119912, and USNM 121157. We have not been able to examine all of these, but CM 5227 (currently identified in the Carnegie Museum database as "*T. elegans*") was collected by José Steinbach in Cochabamba (not Oruro; S. McClaren in litt., 26 January 2010), and USNM 121157 (which we did examine) is unambiguously identifiable as *T. pallidior*. The current identification of MVZ 119912 in the database of the Museum of Vertebrate Zoology (Berkeley) is *T. pallidior*, in agreement with what we would have supposed based on its geographic origin.

SPECIMENS EXAMINED ($N = 43$): **Argentina**—*Jujuy,* Highway 9 at border with Salta (OMNH 29952), Santa Bárbara (AMNH 185323), Yuto (AMNH 186948); *Tucumán,* 12 km WNW Burruyacú along Río Cajón (OMNH 29966), Los Chorillos (OMNH 29976). **Bolivia**—*Chuquisaca,* 3.8 km by road E Carandaytí (AMNH 261245), 2 km SW Monteagudo (MSB 63261, 63262), 9 km by road N Padilla (MSB 63267, 63268), 11 km N and 16 km W Padilla (AMNH 263558, MSB 63269), Porvenir (AMNH 261254, 261255, 261260; MSB 55837), 1.3 km SW Porvenir (AMNH 261264), Río Limón (MSB 63264), 2 km N Tarabuco (AMNH 263556), 4 km N Tarabuco (AMNH 263555), 12 km N and 11 km E Tarabuco (MSB 63265, 63272, 63273); *Cochabamba,* 1.3 km W Jamachuma (AMNH 275427), Parotani (BMNH 2.1.1.118–2.1.1.121 [type series of *venustus*]), 7.5 km SE Rodeo (AMNH 275429, MSB 87100, 87109), Tholapujru (AMNH [uncataloged]), 17 km E Totora (AMNH 275428, MSB 67001); *La Paz,* Caracato (AMNH

TABLE 25
Documented Cases of Sympatry Among Species of *Thylamys*

Locality	Sympatric species[a]
Argentina: Jujuy, 9 km NW Barcena[b]	*T. pallidior* (OMNH 29963) and *T. sponsorius* (OMNH 29974)
Argentina: Mendoza, "Nacunan Reserve"[c]	*T. pusillus* (UWBM 72205) and *T. pallidior* (UWBM 72195)
Bolivia: Chuquisaca, 3.8 km E Carandaytí[b]	*T. pusillus* (AMNH 261268, MSB 55846) and *T. venustus* (AMNH 261245)
Bolivia: Tarija, 3 km SE Cuyambuyo[b]	*T. sponsorius* (AMNH 275448–275450, MSB 67014) and *T. venustus* (AMNH 275436, 275447; NK 23762[d])
Bolivia: Tarija, 8 km S & 10 km E Villa Montes	*T. pusillus* (AMNH 246442–246450) and *T. venustus* (AMNH 246451)

[a]Museum catalog number(s) of exemplar specimen(s) in parentheses.
[b]See gazetteer (appendix 1) for geographic coordinates.
[c]Reserva Biósfera de Ñacuñán (ca. 34°S, 68°W).
[d]Tissue number (voucher not seen).
[e]Villa Montes is at 21°15′S, 63°30′W.

248704, 248705); *Santa Cruz,* Cerro Itahuaticua (MSB 63260), 5 km by road SE Comarapa (AMNH 260030), 15 km NE Quiñe (MSB 87106), 6 km NNE Quiñe (MSB 87107), 17 km S Quiñe (MSB 67003), Río Ariruma (AMNH 275433), 5.5 km by road NE Vallegrande (MSB 67005), 5.5 km by road NNW Vallegrande (MSB 67004); *Tarija,* 1 km S Camatindy (MSB 67007), 3 km WNW Carapari (MSB 67392), Tapecua (MSB 67008).

DISCUSSION

This report and several other recent morphological and molecular studies (especially Solari, 2003; Braun et al., 2005; Carmignotto and Monfort, 2006), convincingly refute Hershkovitz's (1959) hypothesis that all of the taxa currently referred to *Thylamys* are conspecific. Contrary to his assessment (which was not based on any substantive analysis of character data), the existence of multiple species is clearly indicated by diagnostic morphological differences and high sequence divergence (up to 16% in uncorrected pairwise cytochrome-*b* comparisons; table 6) among numerous robustly supported mitochondrial clades. Whereas some of the species recognized as valid in this report are allopatric, others are known to occur sympatrically in various combinations (table 25), providing additional support for the notion that these are evolutionarily independent (reproductively isolated) lineages.

Indeed, many of the vexing problems that previously hampered taxonomic understanding of the genus are now resolved beyond any reasonable doubt. For example, our results unambiguously support Palma and Yates' (1998) hypothesis that *T. venustus* is a distinct species from *T. elegans*, Carmignotto and Monfort's (2006) conclusion that *T. karimii* is a distinct species from both *T. pusillus* and *T. velutinus*, and Solari's (2003) treatment of *T. tatei* as a distinct species from *T. elegans*. On the other hand, several problematic issues remain, among them the probable existence of unnamed forms of the Elegans Group in western Peru, the taxonomic status of allopatric haplogroups that we synonymize with *T. pusillus*, and the morphological diagnosability of geographically overlapping sister taxa that we recognize as *T. venustus* and *T. sponsorius*. In our opinion, these enigmas are unlikely to be resolved to anyone's satisfaction until additional data (e.g., better geographic sampling, nuclear-gene sequences, new morphological characters) become available.

Despite the fact that a few key nodes remain weakly supported, phylogenetic relationships among species of *Thylamys* are completely resolved by the mitochondrial sequence data analyzed in this report (fig. 11). Because this is the first phylogenetic study to include all of the valid species of *Thylamys*, our results provide a uniquely appropriate framework for biogeographic inference. Although a formal analysis of

ecogeographic trait evolution in the genus will be provided elsewhere, some preliminary inferences are appropriately mentioned here.

The first concerns the constraining role of the Andes, the principal topographic feature of the South American continent. All of the closest outgroups to *Thylamys* (e.g., *Chacodelphys* and *Lestodelphys*; see Voss and Jansa, 2009) occur east of the Andes, as does the subgenus *Xerodelphys*, *T. (Thylamys) macrurus*, the entire Venustus Group, and *T. (T.) pusillus,* so the most recent common ancestor of *Thylamys* was almost certainly also cis-Andean. Additionally, our phylogenetic topology suggests that that the Andes were initially traversed by the ancestral lineage of the Elegans Group, and that a single lineage of *T. pallidior* subsequently reinvaded the eastern lowlands (fig. 12). The almost complete absence of phylogeographic structure in haplogroup B of *T. pallidior* (fig. 4) suggests that its cis-Andean range expansion was both rapid and relatively recent.

Among the species of *Thylamys* that occur east of the Andes, our results do not support the east-to-west speciation sequence postulated by Palma et al. (2002). Although Palma et al.'s hypothesis was consistent with a recovered phylogenetic topology that showed a clear east-to-west progression among the five species included in their analysis (*T. macrurus* (*T. pusillus* (*T. venustus* (*T. pallidior* + *T. elegans*)))), no such progression is discernable in our more densely taxon-sampled trees (figs. 3, 11) which, correspondingly, suggest more complex biogeographic scenarios. A key factor in developing new scenarios that more accurately depict relevant processes (dispersal, vicariance, speciation, and extinction) in a meaningful geographic context is the improved resolution of species distributions enabled by recent revisionary work.

Whereas most published range maps suggest that *Thylamys* species are widely distributed and eurytopic, the pattern that is now beginning to emerge from the fog of past misidentifications and erroneous synonymies is that at least some species are narrowly restricted to one or a few macrohabitats. For example, the geographic range of *T. pusillus*—formerly depicted as encompassing the Caatinga, Cerrado, Chaco, Monte Desert, Pampas, and Yungas (e.g., by Brown, 2004: fig. 88)—now appears to be largely restricted to the Chaco (fig. 19). In effect, revised specimen-based identifications have dramatically improved the correspondence between species' geographic ranges and macrohabitat distributions in most cases.

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Fig. 19. *Thylamys pusillus* localities mapped by Brown (2004) with reidentifications based on our examination of museum specimens (see text footnote 3). The "Dry Chaco" ecoregion is coded according to Olson et al. (2001).

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APPENDIX 1

Gazetteer of Sequenced Specimens

Below we list all of the localities from which specimens of *Thylamys* were sequenced for this report. Italicized place names are those of the largest political units (states, departments, or provinces) within each country. Units of distance (kilometers [km] or miles [mi]) are those recorded by the collector. Geographic coordinates (in decimal degrees) and elevation above sea level (if known, recorded in meters [m] or feet [ft]) are given in parentheses. Except as noted otherwise, geographic coordinates for most Argentinian, Chilean, and Peruvian localities were obtained from collector's labels or online collection databases, but Bolivian coordinate data were obtained from Anderson (1997).

ARGENTINA

1. *Buenos Aires,* Campamento Base, Sierra de la Ventana (38.069°S, 62.023°W; 50 m).
2. *Catamarca,* Chumbicha, 0.5 km E Highway 38 on Highway 60 (28.867°S, 66.233°W; 1500 ft).
3. *Catamarca,* 17 km N Barranca Larga (26.853°S, 66.755°W; 3219 m).
4. *Catamarca,* Bella Vista (28.627°S, 65.497°W; 974 m).
5. *Catamarca,* 34.6 km by road W Fiambala (27.704°S, 67.883°W; 7902 ft).
6. *Catamarca,* 5 km S Las Higuerillas on Highway 9 (27.828°S, 65.850°W; 3580 ft).
7. *Catamarca,* 7 km SW Los Morteros (28.639°S, 65.606°W; 1424 m).
8. *Córdoba,* La Tapera, Pampa de Achala (31.622°S, 64.911°W; 1959 m).
9. *Corrientes,* Goya (29.133°S, 59.267°W; 37 m [Paynter, 1995]).
10. *Entre Ríos,* Estancia Santa Ana de Carpinchorí (30.796°S, 58.644°W; 134 m).
11. *Jujuy,* 9 km NW Barcena (24.118°S, 65.500°W; 2655 m).
12. *Jujuy,* Highway 9 at border with Salta, at campground on the way to El Carmen (24.470°S, 65.366°W; 4600 ft).
13. *Jujuy,* 11 km E Humahuaca and 2 km E Pucará on road to Cianzo (23.200°S, 65.243°W; 11,500 ft).
14. *Jujuy,* Santa Bárbara (23.600°S, 65.067°W; 1800 m [Paynter, 1995]).
15. *Jujuy,* 24.8 km E Santa Clara (24.296°S, 64.485°W; 1321 m).
16. *Jujuy,* 8.2 km S Sey (24.013°S, 66.515°W; 4167 m).
17. *Jujuy,* 10 km W Tiraxi on Highway 29 (23.917°S, 65.448°W; 5800 ft).
18. *Jujuy,* Yuto (23.633°S, 64.467°W; 349 m [Paynter, 1995]).
19. *La Rioja,* 15 km N Villa San José de Vinchina (28.717°S, 68.293°W; 1681 m).
20. *Mendoza,* 3 km W Refugio Militar General Alvarado (34.270°S, 69.363°W).
21. *Mendoza,* Salinas del Diamante RR Station (34.967°S, 68.833°W).
22. *Misiones,* Dos de Mayo (27.033°S, 54.650°W; ca. 300 m [Paynter, 1995]).
23. *Neuquén,* Cerrito Piñón, Estancia Collon Cura (40.249°S, 70.632°W; 608 m).
24. *Neuquén,* 0.58 km W and 4.2 km N Cerro Mellizo Sud, Parque Nacional Laguna Blanca (39.050°S, 70.383°W; 1315 m).
25. *Salta,* 16 km S and 1.8 km W Barrancas, along Río de las Burras (23.416°S, 66.206°W; 3521 m).
26. *Salta,* 17 km NW Cachi (25.022°S, 66.238°W; 10,350 ft).
27. *Salta,* 25 km SE La Viña (25.648°S, 65.482°W; 1579 m).
28. *Salta,* Los Sauces (25.787°S, 65.966°W; 5544 ft).
29. *Salta,* 5 km NW Pulares (25.091°S, 65.614°W; 4760 ft).
30. *San Juan,* Castaño Nuevo, 9 km NW Villa Nueva (31.015°S, 69.570°W; 5040 ft).
31. *San Juan,* 8 km W Complejo Astronómico El Leoncito (31.783°S, 69.418°W).
32. *San Luis,* Río Gomes, 7 km E San Francisco del Monte de Oro (32.600°S, 66.059°W; 2800 ft).
33. *San Luis,* 12 km by road N Varela (34.008°S, 66.450°W; 2200 ft).
34. *San Luis,* 15 km E Salinas del Bebedero (33.533°S, 66.488°W; 1350 ft).
35. *Santiago del Estero,* Salinas de Ambargasta, ca. 8 km SE Cerro Rico (29.067°S, 64.633°W; 141 m).
36. *Santiago del Estero,* Virgen del Valle picnic area on Highway 64 (28.133°S, 64.833°W; 2300 ft).
37. *Tucumán,* 5 km N Las Higuerillas on Highway 308 (27.738°S, 65.850°W; 2900 ft).
38. *Tucumán,* Biological Reserve at Horco Molle (26.750°S, 65.350°W; 2400 ft).
39. *Tucumán,* Km 42 on Highway 364 S of San Pedro de Colalao (26.456°S, 65.517°W; 4700 ft).
40. *Tucumán,* Los Chorillos, 13 km NO, limite norte Estancia Los Chorillos (26.350°S, 64.917°W).
41. *Tucumán,* Piedra Tendida, 12 km WNW Burruyacú along Río Cajón (26.459°S, 64.861°W; 2500 ft).
42. *Tucumán,* Reserva La Florida, 7 km W Ibatín, Río Pueblo Viejo (27.192°S, 65.668°W; 515 m).
43. *Tucumán,* 5 km SW Siambón (26.769°S, 65.471°W; 3100 ft).

BOLIVIA

44. *Chuquisaca,* 3.8 km by road E Carandaytí (20.767°S, 63.050°W; 460–480 m).
45. *Chuquisaca,* 68 km by road N Comargo (20.150°S, 65.283°W; 3400 m).
46. *Chuquisaca,* 2 km SW Monteagudo (19.817°S, 63.967°W; 1130 m).
47. *Chuquisaca,* 9 km by road N Padilla (19.300°S, 64.367°W; 2000–2100 m).
48. *Chuquisaca,* 11 km N and 16 km W Padilla (19.200°S, 64.450°W; 2050 m).
49. *Chuquisaca,* Porvenir (20.750°S, 63.217°W; 675 m).

50. *Chuquisaca,* 1.3 km SW Porvenir (20.760°S, 63.229°W; 675 m).
51. *Chuquisaca,* Río Limón (19.550°S, 64.133°W; 1300 m).
52. *Chuquisaca,* 2 km N Tarabuco (19.167°S, 64.933°W; 3250 m).
53. *Chuquisaca,* 4 km N Tarabuco (19.133°S, 64.933°W; 3250 m).
54. *Chuquisaca,* 12 km N and 11 km E Tarabuco (19.067°S, 64.817°W; 2450 m).
55. *Cochabamba,* 1.3 km W Jamachuma (17.533°S, 66.117°W; 2800 m).
56. *Cochabamba,* 7.5 km SE Rodeo (17.683°S, 65.600°W; 3800–4000 m).
57. *Cochabamba,* Tholapujru, camino a Laph'ia (17.300°S, 66.217°W; 11,108 ft).
58. *Cochabamba,* Tinkusiri, 17 km E Totora (17.750°S, 65.033°W; 2950 m).
59. *La Paz,* Caracato (16.983°S, 67.817°W; 2900 m).
60. *Santa Cruz,* Cerro Itahuaticua (19.800°S, 63.517°W; 810 m).
61. *Santa Cruz,* 5 km by road SE Comarapa (17.967°S, 64.483°W; 1695 m).
62. *Santa Cruz,* 15 km NE Quiñe (18.050°S, 64.317°W; 1900 m).
63. *Santa Cruz,* 6 km NNE Quiñe (18.033°S, 64.317°W; 1975 m).
64. *Santa Cruz,* 17 km S Quiñe (18.200°S, 64.300°W; 2100 m).
65. *Santa Cruz,* Río Ariruma, 7 km by road SE Ariruma (18.400°S, 64.317°W; 1750 m).
66. *Santa Cruz,* Tita (18.250°S, 62.100°W; 300 m).
67. *Santa Cruz,* 5.5 km by road NE Vallegrande (18.467°S, 64.133°W; 1800 m).
68. *Santa Cruz,* 5.5 km by road NNW Vallegrande (18.417°S, 64.133°W; 1800 m).
69. *Tarija,* 1 km S Camatindy (21.000°S, 63.383°W; 650 m).
70. *Tarija,* 3 km WNW Carapari (21.800°S, 63.783°W; 850 m).
71. *Tarija,* Carlazo (21.470°S, 64.530°W; 2300–2400 m).
72. *Tarija,* Chuquiaca (21.783°S, 64.094°W; 890 m).
73. *Tarija,* roadside above Cieneguillas (21.317°S, 65.033°W; 3400 m).
74. *Tarija,* 3 km SE Cuyambuyo (22.267°S, 64.550°W; 900 m).
75. *Tarija,* 5 km NNW Entre Ríos (21.483°S, 64.200°W; 1600 m).
76. *Tarija,* Estancia Bolívar (21.633°S, 62.567°W).
77. *Tarija,* 5 km W Estancia Bolívar (21.633°S, 62.617°W).
78. *Tarija,* 4.5 km E Iscayachi (21.483°S, 64.917°W; 3750 m).
79. *Tarija,* ca. 10 km by road W Narvaez (21.383°S, 64.292°W, 2220 m).
80. *Tarija,* 11.5 km N and 5.5 km E Padcaya (21.783°S, 64.667°W; 1900 m).
81. *Tarija,* Serranía Sama (21.450°S, 64.867°W; 3200 m).
82. *Tarija,* Tapecua (21.433°S, 63.917°W; 1500 m).
83. *Tarija,* 1 km E of Tucumilla (21.450°S, 64.817°W, 2500 m).

BRAZIL

84. *Distrito Federal,* Brasilia, Jardin Botãnico (15.783°S, 47.917°W; 1100 m [Paynter and Traylor, 1991]).
85. *Distrito Federal,* 25 km S Brasilia, IBGE (16.009°S, 47.917°W).
86. *Mato Grosso do Sul,* Fazenda Califórnia (20.683°S, 56.867°W; 650 m).
87. *Tocantins,* Rio da Conceição (11.184°S, 46.844°W).

CHILE

88. *Coquimbo,* Limarí, Parque Nacional Fray Jorge (30.667°S, 71.667°W).
89. *Región Metropolitana de Santiago,* Las Condes, San Carlos de Apoquindo (33.404°S, 70.484°W; 3743 ft).
90. *Región Metropolitana de Santiago,* Santiago, Maipu, Rinconada de Maipu (33.495°S, 70.894°W; 555 m).
91. *Tarapacá,* Iquique, Colchane, Enquelga (19.220°S, 68.745°W; 3960 m).
92. *Valparaíso,* La Campana National Park, Palmas de Ocoa (32.950°S, 71.083°W).
93. *Valparaíso,* Zapalla, Quebrada del Tigre (32.560°S, 71.439°W, 280 m).

PARAGUAY

94. *Concepción,* 7 km NE de Concepción, Escuela Agropecuaria (23.350°S, 57.383°W).
95. *Alto Paraguay,* Fortín Pikyrenda (20.083°S, 61.783°W; 420 m).
96. *Boquerón,* Parque Nacional Teniente Enciso (21.050°S, 61.750°W).

PERU

97. *Ancash,* 1 km N and 12 km E Pariacoto (9.501°S, 77.774°W; 8500 ft).
98. *Arequipa,* 3 mi W Atico (16.233°S, 73.650°W; 100 ft).
99. *Arequipa,* 1 km N Chivay (15.631°S, 71.600°W; 3700 m).
100. *Arequipa,* 3 mi N Mollendo (16.976°S, 72.049°W; 100 ft).
101. *Ayacucho,* 15 mi WNW Puquio (14.617°S, 74.339°W; 12,000 ft).
102. *Lima,* 1 mi W Canta (11.467°S, 76.639°W; 8800 ft).
103. *Lima,* 8 mi NE Yauyos (12.368°S, 75.866°W; 9500 ft).
104. *Tacna,* 65 km W Tacna (17.764°S, 70.747°W; 300 ft).
105. *Tacna,* 4 km N Tarata (17.438°S, 70.033°W; 12,800 ft).

APPENDIX 2.
Primers Used for Amplification of CYTB, COX2, and ND2

Name[a]	Sequence
CYTB-F1-Didelphidae	5′-ATAACCTATGGCATGAAAAACCATTGTTG
CYTB-R1-Didelphidae	5′-GCCTTGTAAGCCAGCAATGAAGG
CYTB-420R-Didelphidae	5′-TGAGGACAAATATCCTTCTGAGGAGC
CYTB-670F-*Thylamys*	5′-GATCCTGTTTCGTGRAGGAA
CYTB-770R-*Thylamys*	5′-TAGGAGACCCTGAYAACTTCAC
CYTB-830R-*Thylamys*	5′-GGCAAATAGAAARTATCACTCTGG
CYTB-1000R-*Thylamys*	5′-ACWGGTTGTCCYCCAATTCA
CYTB-170F-*elegans*	5′-CCTAGCCATACATTACACATCAG
CYTB-260R-*elegans*	5′-CGAAACATTCACGCTAATGGAGC
CYTB-270F-*elegans*	5′-AAACATTCACGCYAATGGAGCYTCAAT
CYTB-340F-*elegans*	5′-CCGAGGACTTTATTATGGATCTTA
CYTB-560F-*elegans*	5′-GCAAAGAATCGGGTAAGTGTAGC
CYTB-620R-*elegans*	5′-TTCCTTCACGAAACAGGATC
CYTB-700F-*elegans*	5′-CACCCCTACTACACTATTAAAGA
CYTB-800R-*elegans*	5′-GCTAACCCACTCAATACCCCTCC
CYTB-900F-*elegans*	5′-CCCAAACAAATTAGGAGGTGT
CYTB-930R-*elegans*	5′-CCACTACTTCATACATCAAACCAAC
CYTB-1030F-*elegans*	5′-CAGCCAATCTTCTAATTTTAACCTG
CYTB-1150R-*elegans*	5′-CTTCAACCAAAATACCCTTAACAT
CYTB-200F-*karimii*	5′-GCTATACACTACACATCGGAC
CYTB-215R-*karimii*	5′-CAGTAGCACATATCTGCCGAGA
CYTB-410F-*karimii*	5′-TAACAGTTATAGCTACCGCATTTG
CYTB-460R-*karimii*	5′-TACAAATCTTCTATCAGCTATTCC
CYTB-630F-*karimii*	5′-CCTGTCTCGTGGAGAAATAGT
CYTB-660R-*karimii*	5′-AACCCAGATTCAGATAAAATCCC
CYTB-810F-*karimii*	5′-ACACCAGCTAACCCACTCAA
CYTB-850R-*karimii*	5′-GCCTATGCAATCCTACGATC
CYTB-990F-*karimii*	5′-TATTCCGACCAATCTCACAAAC
CYTB-1020R-*karimii*	5′-ATCCTAACTTGAATCGGAGGACA
CYTB-501R-*macrurus*	5′-AGTGAATTTGAGGTGGTTTCTCAG
CYTB-530F-*pallidior*	5′-GAATGAATTTGAGGTGGGTTCTCAG
CYTB-940R-*pallidior*	5′-CTTCATACATCAAACCAACGAA
CYTB-320F-*sponsorius*	5′-GCCGAGGGATCTATTACGGA
CYTB-910R-*sponsorius*	5′-AGGAGGAGTTCTAGCACTATTAGC
CYTB-225F-*venustus*	5′-CTGCTTTCTCCTCAGTAGCTCA
CYTB-265R-*venustus*	5′-TATTCATGCTAAYGGRGCTTCT
CYTB-240F-*venustus*	5′-TGCCGAGATGTAAATTTCGGATGA
CYTB-260F-*venustus*	5′-TATTCATGCTAAYGGRGCTTCT
CYTB-285F-*venustus*	5′-GGGRCTTCTATATTTTTTATGTG
CYTB-665R-*velutinus*	5′-TCAGATAAAATCCCCTTCCACCC
CYTB-190F-*velutinus*	5′-CTTAGCCATGCACTACACATC
CYTB-230F-*Lestodelphys*	5′-CGAGACGTAAATTATGGGTGATTAA
COX2-F1-*Thylamys*	5′-ATTTCAAGTCAAYCCCATAACC
COX2-R1-*Thylamys*	5′-CTCCTCAAAACAACATGCCACA
COX2-500F-*Thylamys*	5′-TGAGCAGTTCCATCCTTAGG
ND2-F1-*Thylamys*	5′-CCATACCCCGAAAATGTTGGTT
ND2-R1-*Thylamys*	5′-CGAACGCAAATCGAACGCTT
ND2-790F-*Thylamys*	5′-CYCCACTTACAGGTTTTATACCYAAA

[a]Each primer name consists of three parts. First, the locus is indicated. Next, the position of the primer relative to the 5′ end of the locus and the orientation of the primer (forward or reverse) is indicated. "F1" and "R1" designations refer to whole-locus forward and reverse primers. The third component of each name refers to the taxon to which each primer was optimized.